



## Small mammal responses to forest management for oak regeneration in southern Indiana

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### ABSTRACT

We used a 5-decade chronosequence of harvest openings to characterize population and community-level responses of small mammals to forest management targeting oak regeneration in southern Indiana. Live-trapping at 42 different sites allowed modeling of occupancy and relative abundance using environmental covariates while incorporating imperfect detection. Species richness was higher in smaller openings on southwest-facing aspects. Similarity between species richness of different age classes decreased with increasing site age. Eastern chipmunk (*Tamias striatus*) relative abundance was greater in early seral stages, i.e., at young sites with low basal areas. Relative abundance of white-footed mice (*Peromyscus leucopus*) exhibited different responses to coarse woody debris on sites versus microsites. Pine voles (*Microtus pinetorum*) and short-tailed shrews (*Blarina brevicauda*) were more likely to occupy older sites. We observed a greater relative abundance of short-tailed shrews at sites with steep and northeast-facing slopes. Northeast-facing slopes also resulted in higher short-tailed shrew occupancy rates. Incorporating detection probability enabled us to derive more accurate estimates of relative abundance and, when coupled with a Bayesian framework, permitted the estimation of occupancy for uncommon species. Our estimated responses can be used by forest managers to determine the potential impacts of even-aged and uneven-aged oak management on small mammals, and the statistical methodology we used can be applied even more broadly to improve understanding of wildlife responses to forest management.

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### 1. Introduction

Oak-hickory (*Quercus-Carya*) hardwood stands influence biodiversity, energy flow, nutrient dynamics, and hydrology of landscapes (Ellison et al., 2005; Johnson et al., 2002; McShea and Healy, 2002). Oak and hickory are important in regulating wildlife through mast, which supplies a critical energy source during winter months and positively influences small mammal abundance (Clotfelter et al., 2007; Jones et al., 1998; McShea et al., 2007; Smith and Scarlett, 1987; Wolff, 1996). Oak-hickory mast has increased in importance due to the disappearance of American chestnut (*Castanea dentata*) during the first half of the 20th century and the current decline of American beech (*Fagus grandifolia*) (Healy et al., 1997; McShea et al., 2007).

Over the past several decades, suppression of fire regimes has produced conditions favoring late successional, shade tolerant species such as maple (*Acer* spp.) in the understory instead

of disturbance-dependent, shade-intolerant oak (Abrams, 1992, 2003; Cho and Boerner, 1991; Fralish, 1988, 1997; Fralish and McArde, 2009). Considerable research has focused on forest management strategies to reverse declines in oak regeneration (Albrecht and McCarthy, 2006; Brudvig, 2008; Povak et al., 2008). An important corollary of this work is to develop a greater understanding of wildlife responses to these management strategies.

Small mammals are important components of forest ecosystems, where they function as primary and secondary consumers, dispersers of seeds and mycorrhizal fungi (Maser et al., 1978; Moore et al., 2007), staple items of prey for numerous vertebrate predators (Whitaker and Hamilton, 1998) and agents of soil aeration and enrichment (Abaturov, 1972; Bakker et al., 2004; Hole, 1981). As primary consumers, they are also important for managers to monitor due to their potentially negative impact on tree regeneration. Studies examining responses of small mammals to clearcuts, an approach commonly applied to regenerate oak (Hannah, 1987), have produced mixed results. In eastern deciduous forests, white-footed mice, *Peromyscus leucopus*, appear to respond in a neutral or positive manner shortly following clearcutting, although negative responses were reported in two studies (Fantz and Renken, 2005; Healy and Brooks, 1998; Schmid-Holmes and Drickamer,

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2001, review by Kirkland, 1990). Eastern chipmunks, *Tamias striatus*, exhibited both negative and positive numerical responses at latitudes slightly north of southcentral Indiana, the area in which we conducted our study (Kirkland, 1990). Measured short-term effects of harvest on short-tailed shrews, *Blarina brevicauda*, generally have been neutral or negative (Ford et al., 1997; Healy and Brooks, 1998; Kirkland, 1977a,b, but see Mitchell et al., 1997). Responses of various species of *Sorex* have tended toward neutral or positive, with exceptions (Kirkland, 1990). Fewer studies have examined the effects of uneven-aged management on small mammal populations. Soricid abundance did not change with partial over-story removal (Ford and Rodrigue, 2001). *Peromyscus* spp. exhibited positive responses shortly after uneven-aged harvests (Fantz and Renken, 2005).

The inability to infer general patterns of small mammal responses to even- and uneven-aged management of hardwood stands in prior studies may reflect temporal or spatial variation in factors regulating demography. Alternatively, general patterns in mammalian responses may have been masked in part by methodological shortcomings of these studies. Specifically, the studies cited in the previous paragraph used number of individuals captured, or captures per unit of effort, as population and community response variables. Because trapping yields a count of individuals detected,  $C$ , a canonical estimate of population size,  $N$ , can be expressed as  $N=C/\beta$ , where  $\beta$  is the probability of detecting an individual in the population (Williams et al., 2002, p. 244). Likewise, trapping yields a count of species detected,  $K$ , resulting in a canonical estimator of species richness,  $S=K/p$ , where  $p$  is the probability of detecting a species, given its occurrence in the community (Williams et al., 2002, p. 556). By failing to incorporate explicitly  $\beta$  and  $p$ , prior analyses of small mammal responses to timber harvest have assumed that probability of detection does not vary among sites or species. Unfortunately assuming perfect or homogeneous detection can lead to substantial bias (e.g., MacKenzie et al., 2006; Nichols, 1992). In addition, prior studies often have focused on common species because sample sizes associated with rarer species were too small to warrant conventional analyses (e.g., Fantz and Renken, 2005; Schmid-Holmes and Drickamer, 2001). We addressed each of these issues, thereby overcoming potential deficiencies associated with prior studies.

For analysis of species occupancy patterns and community-level responses to harvest and environmental covariates, we used a hierarchical Bayesian (HB) multi-species site occupancy model that also accounts explicitly for imperfect detection of species (Russell et al., 2009). The model allows for estimation of occupancy and detection rates for each individual species, incorporation of site- and species-level covariates, and approximation of the uncertainty associated with parameter estimates. An important advantage of the multi-species model of Russell et al. (2009) is its hierarchical structure, because it affords increased precision of estimators due to the sharing of information across species; i.e., the structure provides a composite estimate that applies to the community of observed species versus only those species that meet some arbitrary sample size threshold (Sauer and Link, 2002). For comparison of population responses, we incorporated detection probability using the abundance model of Royle and Nichols (2003) and bootstrapped encounter histories to obtain site-specific estimates of precision (Buckland et al., 2009).

Our objective is to characterize population and community responses of small mammals to forest stands managed for oak regeneration in southern Indiana. By using improved occupancy and abundance estimation methods that incorporate probability of detection, we derived more accurate estimates for a larger number of species than in prior studies. We hypothesize that when using these methods rodent populations will have higher abundances

and shrew populations will have lower abundances in recently harvested openings. Also, we hypothesize that species richness will be greatest in older openings.

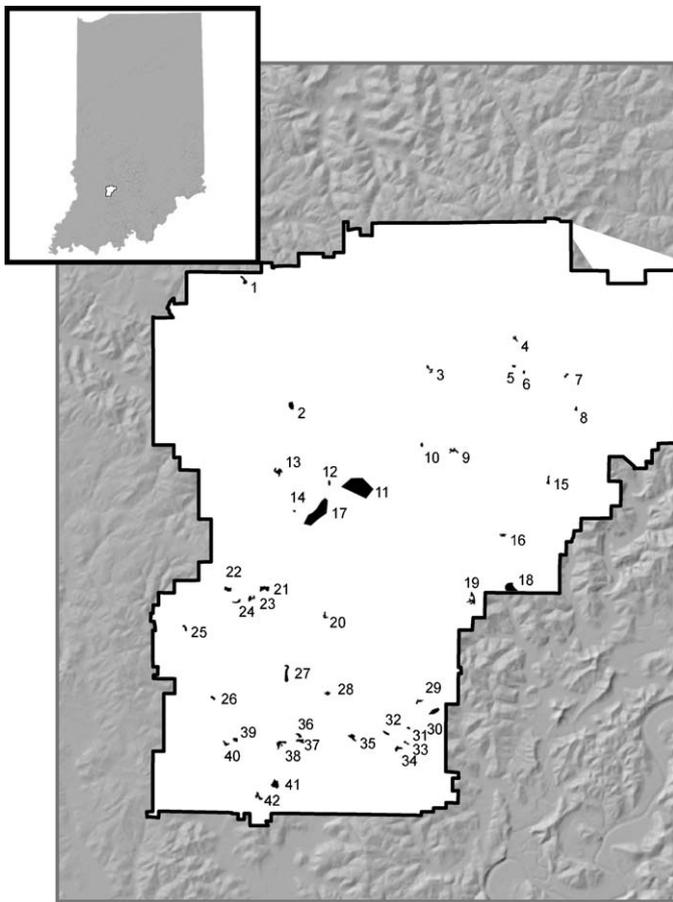
## 2. Materials and methods

### 2.1. Study area

Long-term studies can capture the large fluctuations in population dynamics of small mammals often missed by shorter-term research, but their cost can be prohibitive (Swihart and Slade, 1990). Chronosequences offer an alternative to longitudinal studies and can lead to working hypotheses regarding wildlife responses to forest management. A chronosequence involves sampling sites of similar habitat types that have had similar forest management treatments applied to them at varying times. Thus, sites of varying ages after treatment are selected for study and are representative of different seral stages (Fernandez et al., 1994; Ford et al., 2002; Homyack et al., 2005; Stuart-Smith et al., 2006). Chronosequences allow insights into responses developing over decades by taking a “snapshot” of conditions for sites of varying ages over a short period of time.

We sampled small mammals along a harvest chronosequence at Crane Naval Surface Warfare Center (NSWC) located in Martin County, IN (38°52'00"N/86°50'00"W). NSWC was first established in 1935 as a state forest and was later expanded to its current size (255 km<sup>2</sup>) by the U.S. Navy in 1941. Before NSWC establishment, the land had been cleared by farmers using fire to permit agriculture and grazing. From 1940 to 1950, most of NSWC was allowed to succeed to forest. During this time, contracts for crop tree releases, such as cleanings and improvement cuttings, were used to reduce oak competitors at NSWC. These contract incentives, along with the previous human disturbances, encouraged high amounts of oak regeneration (T. Osmon, NSWC forester, pers. commun.). Currently, 82.5% of the base is forested, and harvest rates have not changed much since the 1950s. Approximately 1300–1500 ha per year are harvested, with about 180–200 ha in openings. As the NSWC forest matured, management practices before the 1990s had limited success in maintaining the high oak density due to a high proliferation of yellow poplar, *Liriodendron tulipifera*, and lack of human disturbance. Current harvest practices focus on clearcuts >2 ha and single-tree or group selection cuts ≤2 ha on south- or west-facing slopes to encourage oak regeneration. Occasional post-harvest timber stand improvement includes releasing oak seedlings 10 and 20 years after the initial cut, creating snags out of competing tree species and leaving all downed woody debris (T. Osmon, pers. commun.).

We selected six post-harvest age classes for sampling across the chronosequence: 1–2, 4–6, 8–10, 12–16, 27–33, and >40 years. The stands >40 years old have not been harvested since NSWC inception. Eight sample sites of each age class were chosen randomly from a larger set of possible sites using a GIS data layer. Within each age class, selected sites were constrained further to fall into two area classes (0.8–1.6 ha and 1.7–8.1 ha) and two aspects (northeast-facing slope, 5–85° azimuth, and southwest-facing slope, 185–265° azimuth). The small area class was comprised of group selection stands within a larger mature stand with an uneven-aged management regime. The larger area class was comprised of even-aged clearcuts created to replace an entire stand. The sampling design thus consisted of 6 age classes × 2 size classes × 2 aspects. Not all 48 age × size × aspect combinations were found within NSWC. Consequently, a total of 42 sample sites were chosen, with 22 sites sampled in 2007 and 20 in 2008 (Fig. 1). Additionally, one sample site from each of the six age classes was chosen for sampling in both years to assess inter-annual variation.



**Fig. 1.** The 42 small mammal trapping site locations at Crane Naval Surface Warfare Center located in Crane, Indiana. Six different age classes, two different aspects, and two different size even-aged cuts were chosen for sampling. Forest management goals at these sites target oak (*Quercus* spp.) regeneration.

## 2.2. Mammal sampling

One small mammal grid was placed in the center of each of the 42 sample sites. The mammal grids consisted of 25 trap stations arranged in a lattice with adjacent stations separated by 20 m and at least 20 m from the edge of the harvest opening. Every trapping point received a Sherman trap (H.B. Sherman Trap, Inc., Tallahassee Fla.) and every other trapping point, 12 in total per grid, received a sunken trap. The sunken traps were composed of 16.5 × 15.9 cm aluminum cans with small perforations for drainage. Sherman and sunken traps were placed within 1.0 and 1.5 m, respectively, of the center of a trap station. Sunken traps were situated whenever possible along a natural drift fence such as a fallen log. Due to disturbance caused by raccoons (*Procyon lotor*) and opossums (*Didelphis virginiana*), Tomahawk traps (Tomahawk Live Traps Co., Tomahawk, WI) were placed in each corner of a trapping grid and baited with cat food. All captured raccoons and opossums were relocated at least 10 km away from a sample site.

Sherman traps were pre-baited for 3 days before trapping. Small mammals were habituated to sunken traps during the pre-baiting period by placing a plastic lid over the trap and then covering it with leaf litter. Following pre-baiting, traps were set and checked for 5 consecutive days, both in the morning and evening. Sherman traps were baited with a mixture of sunflower seeds and rolled oats, and sunken traps were provisioned with earthworms.

For each captured individual, species, weight, sex, and reproductive status were recorded. Rodents were considered reproductively

active if they were lactating or had an enlarged pubic symphysis (females) or descended testes (males). Shrews were toe clipped for identification. In 2008, rodents at four of the NSWC sites also received individual ear tags so we could assess the degree to which our estimates of relative abundance derived from capture data corresponded with absolute estimates of abundance using mark-recapture methods. All trapping and handling procedures were approved by the Purdue Animal Care and Use Committee (protocol #07-045).

## 2.3. Vegetation sampling

For each harvest site, a short description was recorded. Presence or absence of standing/flowing water was noted. At the center of the harvest area, percent slope was estimated using a clinometer, and plot aspect was estimated in degrees using a compass. Slope position and shape also were determined using pre-defined classifications (Ruhe, 1975). Within an 11.4 m radius (0.04 ha) from plot center, all trees >5 cm diameter at breast height (dbh) were identified to species and dbh measured. For all coarse woody debris >10 cm diameter at its midpoint, length, midpoint diameter, and decay class (Maser et al., 1979) were recorded.

Vegetative structure also was recorded at the center of each harvest area. At the cardinal points of a circle of radius 3.6 m (0.004 ha) from the center of the harvest area, a 1 m<sup>2</sup> quadrat was used to estimate optically the cover of herbaceous plants and seedlings <1 m tall. All saplings <5 cm dbh and >1 m tall were identified to species and counted within the 0.004-ha circle. Each stem was counted for multi-stemmed vegetation.

Canopy structure was sampled at 2 m intervals along four 10-m transects oriented upslope, downslope, and perpendicular to the slope from the center of each harvest area. At each sampling point a density pole was used to measure vegetation density in four vertical strata within 1 m height increments. At each decimeter on the density pole, vegetation within 5 cm of the pole received a tally, and the dominant species was recorded. The density was then determined by summing the number of decimeter contacts (Mills et al., 1991). At the end of each transect, a spherical densiometer was used to estimate canopy cover.

Microsite sampling was done for each small mammal trapping station. At each station, a 1 m radius circle was placed adjacent to the Sherman trap. The percent herbaceous and woody cover for plants <50 cm tall was recorded. At the circle center, depth of the leaf litter was measured. The length of all coarse woody debris >5 cm also was sampled.

## 2.4. Analysis based on occurrence

We used a single season, hierarchical multi-species model of site occupancy that incorporated imperfect detection (Kéry and Royle, 2008; Royle and Dorazio, 2008, pp. 390–393). The model enables estimation of both species- and community-level attributes and also can be used to estimate attributes of the observed community or the number of unobserved species in the community (Kéry and Royle, 2008; Russell et al., 2009). We focused on the former, as we believe that conclusions with management recommendations based on hypothetical unidentified species would be less helpful to practicing professionals (Russell et al., 2009).

The general structure of the hierarchical multi-species model has been described in detail elsewhere (e.g., Royle and Dorazio, 2008, pp. 380–393). Briefly, each of  $R$  (=42) harvest sites is visited on  $J$  (=5) occasions, and for each occasion a record is made of species detected. For each species a count,  $y_k$ , denotes the number of detections of the species in  $J$  visits for site  $k$ . Conditional on the target species' occurrence at site  $k$ , the corresponding  $y_k$  can be modeled as a binomial random variable with  $J$  trials consisting of detection

probability  $p_k$ . The detection frequencies for each of the  $n$  observed species at the  $R$  sites can be summarized conveniently in a matrix  $Y_{n \times R}$ . Species  $i$  occurs with probability  $\psi_i$ . A latent state variable  $z_{ik}$  represents whether the species occurs at the site ( $z_{ik} = 0$ ) or not ( $z_{ik} = 1$ ). Thus, the hierarchical model also includes a matrix  $Z_{n \times R}$  of state variables that are only partially observed. That is, detection of a species at a site signifies occurrence there, but failure to detect a species at a site does not imply its absence at the site. Define  $u_i = \text{logit}(\psi_i)$  and  $v_i = \text{logit}(p_i)$ , where  $\text{logit}(x) = \ln(x/1-x)$ . To model interspecific heterogeneity in  $p$  and  $\psi$ , we assumed a bivariate normal distribution, i.e.,  $u_i \in N(\beta, \sigma_u^2)$ ,  $v_i \in N(\alpha, \sigma_v^2)$ , and covariance  $\sigma_{uv}$ . The parameters  $\beta$  and  $\alpha$  represent the mean probabilities of occurrence and detection, respectively, on a logit scale when considering all observed species in the community (Royle and Dorazio, 2008, p. 382).

The hierarchical model is easily extended to incorporate effects of environmental covariates on  $\psi_{ik}$ , the probability of occurrence of species  $i$  at site  $k$ . Using the notation above,  $z_{ik} | \psi_{ik} \sim \text{Bernoulli}(\psi_{ik})$ , where  $\text{logit}(\psi_{ik})$  is a linear function of site-specific covariates. We considered years since harvest (Age), opening area (Size), and aspect as covariates of occurrence at NSWC. Incorporating covariates into the observation portion of the model required an additional subscript, because detection may differ among species, sites, and sampling occasions. Thus,  $y_{ijk}$  is a binary observation indicating detection ( $y_{ijk} = 1$ ) or not ( $y_{ijk} = 0$ ) of species  $i$  during the  $j$ th visit to site  $k$ . Then  $y_{ijk} | p_{ijk}, z_{ik} \sim \text{Bernoulli}(p_{ijk} z_{ik})$  where  $\text{logit}(p_{ijk})$  is a linear function of site- or time-specific covariates that could influence detection. We considered average daily temperature (Temp), precipitation (Precip), year, trap nights as a measure of sampling effort (Effort), Julian day (JD), and Julian day<sup>2</sup> centered around the mean (JD<sup>2</sup>) as possible covariates of detection at NSWC. All continuous occupancy and detection covariates were standardized prior to analysis.

The single-season, hierarchical, multi-species site-occupancy model was performed within a Bayesian framework. We chose non-informative priors to ensure that inference was driven by data collected during our study. Specifically, we selected priors for the inverse logit of  $\alpha$  and  $\beta$  from uniform distributions over the interval [0,1], priors for  $\sigma_u$  and  $\sigma_v$  from uniform [0,10], and priors for the correlation of  $u$  and  $v$ ,  $\rho = \rho_{uv}/\sigma_u\sigma_v$ , from uniform [-1,1]. The model was implemented in the software package R 2.6.1 (R Development Core Team 2007) using the add-on package R2WinBUGS (Sturtz et al., 2005), which calls the software package WinBUGS (Spiegelhalter et al., 2003; version 1.4.3). WinBUGS uses Markov chain Monte Carlo (MCMC) techniques to derive posterior distributions for model parameters. For each run, we used five parallel chains of length 55,000 and discarded the first 5000 to avoid effects due to random starting values (Kéry and Royle, 2008). A thinning rate of 50 was used to reduce the likelihood of dependent samples (Ntzoufras, 2009). Gelman-Rubin diagnostics were used to assess convergence (Brooks and Gelman, 1998).

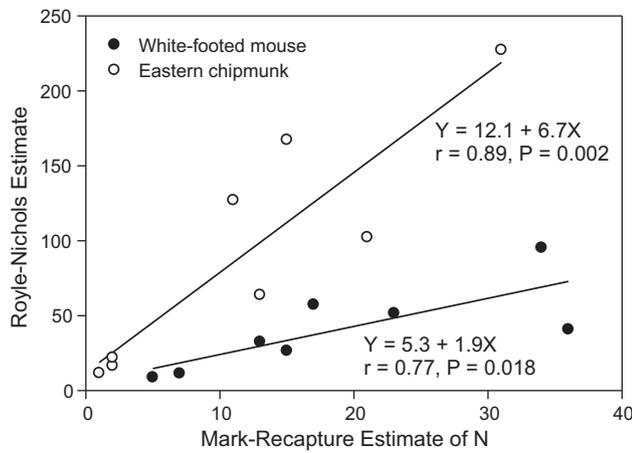
Community-level attributes were derived from the elements of  $Z$ . Species richness was estimated for site  $k$  as  $S_k = \sum_{i=1}^n z_{ik}$ . An estimate of average species richness for a category  $a$  of harvest sites was derived by summing across all sites in the category and then dividing by the  $A$  sites in the category; i.e.,  $\bar{S}_a = \sum_{k \in a} S_k / A$ . Estimates of average species richness were thus obtained for each age, size, and aspect category of harvest sites. The same procedure was used to derive estimates of the average similarity between pairs of categories. We used Jaccard's coefficient (Legendre and Legendre, 1998, p. 256) to measure similarity in species richness between categories  $a$  and  $b$ :  $C_{ab} = S_{a \cap b} / (S_{a \cap b} + S_a + S_b)$ .  $S_{a \cap b}$  represents the number

of species shared by classes  $a$  and  $b$ , whereas  $S_a$  and  $S_b$  are the number of species unique to categories  $a$  and  $b$ , respectively. Thus, total overlap in species yields  $C_{ab} = 1$ , and no shared species yields  $C_{ab} = 0$ .

## 2.5. Analysis based on relative abundance

Royle and Nichols (2003) developed a single-species model incorporating heterogeneity in detection probability with finite mixtures. Suppose that for  $N$  animals at trap location  $k$ , replicate sampling yields a record of the number of individuals detected there. Then the probability of detecting at least one individual at the location, given that the species occurs there, is  $p_k = 1 - (1-r)^{Nk}$ , where  $r$  is the probability of capturing an individual (Royle and Nichols, 2003). Considering abundance as a Poisson random variable, i.e.,  $\Pr(n=n) = e^{-\lambda} \lambda^n / n!$ , where  $\lambda$  is the mean of the Poisson distribution on  $N$ , permits estimation of  $r$  and  $\lambda$  by the method of maximum likelihood (Royle and Nichols, 2003). Use of a Poisson distribution implicitly assumes absence of overdispersion spatially invariant density. Because a single detection model was fitted to observations from all harvest sites, site-specific estimates of density were not independent. Thus, we used the two-stage bootstrap method of Buckland et al. (2009) to quantify precision. We implemented a single-season version of the Royle–Nichols model using PRESENCE 2.4 (Hines, 2006) with species-level detection histories developed for each trap location. For each species we determined the combination of covariates for  $r$  resulting in the smallest Akaike's Information Criterion (AIC) value (Burnham and Anderson, 2002). We then incorporated site-specific covariates for  $\lambda$  and chose the model with lowest AIC. Detection covariates considered for analysis were JD, JD<sup>2</sup>, year, Effort, Temp, and Precip. Site-specific covariates for  $\lambda$  included presence or absence of water (Water), percent canopy cover (Canopy), gradient of the slope (Gradient), number of saplings (>5.1 cm DBH, Sapling), coarse woody debris at the site level (CWD), coarse woody debris at the trap level (Micro CWD), percent herbaceous cover at the trap level (Herb), percent woody cover at the trap level (Wood), basal area (BA), Age, Size, and aspect. Confidence intervals and standard errors for each parameter were estimated using bootstrap re-sampling of encounter histories at trap locations in each harvest site. The selected Royle–Nichols (2003) model was fitted in R 2.6.1 using at least 200 bootstrap samples for each species, resulting in  $200 \times 1210$  trap-specific abundance values. These estimates were used to derive standard errors of  $N$  for each harvest site.

Because our trap spacing likely included multiple sampling stations within a home range, we suspected that our estimates of  $\lambda$  were biased high and likely were more appropriately considered estimates of relative abundance. To validate that the estimates derived from the Royle–Nichols (2003) model could be considered measures of relative abundance, we conducted traditional mark-release-recapture sampling at 4 of the NSWC sites and 4 additional sites located in comparable forest conditions 57 km northeast of NSWC. For each of these sites, we used program CAPTURE (White et al., 1982) to compute estimates of  $N$  for the Chao (1988, 1989) and Chao et al. (1992) estimators under variable detectability due to individual heterogeneity ( $M_h$ ), time ( $M_t$ ), and their combination ( $M_{th}$ ). The Royle–Nichols (2003) estimates of relative abundance at each site were regressed against the corresponding mark-release estimates of  $N$  for eastern chipmunks and white-footed mice, the species for which sufficient sample sizes were obtained. Significant regression relationships between Royle–Nichols estimates of abundance and mark-release estimates of abundance were taken as evidence that the Royle–Nichols model had produced reasonable estimates of relative abundance (Fig. 2).



**Fig. 2.** Validation of estimates derived from the Royle–Nichols abundance model with mark-recapture abundance estimates for eastern chipmunks and white-footed mice.

**Table 1**

Captures of small mammals at Crane Naval Surface Warfare Center. A total of eleven species were captured during the 2007 and 2008 sampling period. Only the seven most common species were used for the occupancy analysis, and the four most common were used for the relative abundance analysis.

Species		2007	2008	Total
Eastern chipmunk	<i>Tamias striatus</i>	793	1243	2036
White-footed mouse	<i>Peromyscus leucopus</i>	375	770	1145
Short-tailed shrew	<i>Blarina brevicauda</i>	145	90	235
Pine vole	<i>Microtus pinetorum</i>	16	30	46
Smoky shrew	<i>Sorex fumeus</i>	10	8	18
Southeastern shrew	<i>Sorex longirostris</i>	3	7	10
Pygmy shrew	<i>Sorex hoyi</i>	2	6	8
Long-tailed weasel	<i>Mustela frenata</i>	0	7	7
Meadow jumping mouse	<i>Zapus hudsonius</i>	0	3	3
Southern flying squirrel	<i>Glaucomys volans</i>	2	1	3
Least weasel	<i>Mustela nivalis</i>	0	1	1

### 3. Results

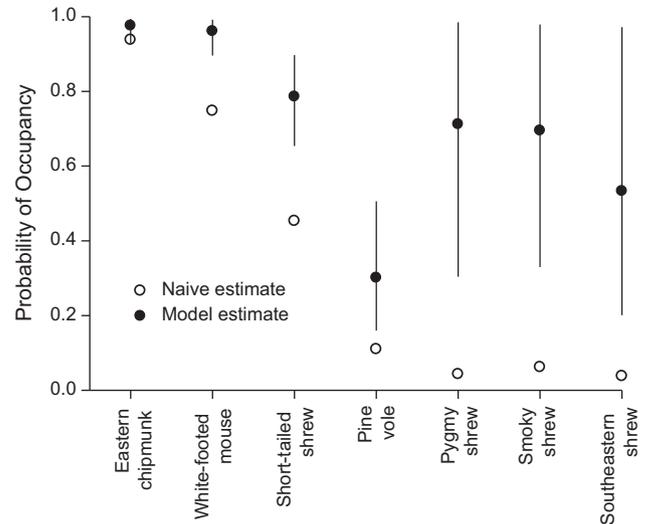
#### 3.1. Trapping results

Trapping took place from 14 May through 29 June 2007 and resulted in a total of eight species caught in 6781 trap nights. In 2008, trapping took place from 12 May to 27 June, with eleven species caught in 8258 trap nights. We captured 2036 eastern chipmunks, 1145 white-footed mice, 235 short-tailed shrews, 46 pine voles (*Microtus pinetorum*), 18 smoky shrews (*Sorex fumeus*), 10 southeastern shrews (*Sorex longirostris*), 8 pygmy shrews (*Sorex hoyi*), 7 long-tailed weasels (*Mustela frenata*), 3 meadow jumping mice (*Zapus hudsonius*), 3 southern flying squirrels (*Glaucomys volans*), and a least weasel (*Mustela nivalis*) (Table 1).

**Table 2**

Results from single-season, hierarchical multi-species occupancy models analyzed within a Bayesian framework. Model included age, aspect, and size occupancy covariates as descriptors of potential forest management practices. The best detection probability covariate included was temperature, as determined by the lowest Deviance Information Criterion. Bold-faced type indicates parameters that did not contain zero within 95% credible intervals.

Covariate	Eastern chipmunk		White-footed mouse		Short-tailed shrew		Pine vole		Smoky shrew		Southeastern shrew		Pygmy shrew	
	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE
$p$														
Temp	0.65	0.38	-0.18	0.20	0.02	0.19	-0.01	0.31	0.08	0.32	-0.21	0.38	-0.46	0.38
$\psi$														
Age	0.52	0.64	0.67	0.63	<b>0.74</b>	<b>0.56</b>	<b>0.72</b>	<b>0.58</b>	0.46	0.86	0.35	0.73	0.69	0.73
Aspect	1.31	1.23	1.45	1.23	<b>1.08</b>	<b>0.82</b>	-0.15	0.85	1.21	1.21	1.03	1.16	0.86	1.26
Size	0.32	0.78	0.48	0.77	0.26	0.49	-0.20	0.45	0.51	0.84	1.16	1.03	0.13	0.97



**Fig. 3.** Estimates of probability of occupancy derived from a single-season, hierarchical multi-species occupancy model for the seven most abundant species of small mammals. Credible intervals (95%) are indicated by vertical lines. Note that the naïve occupancy estimates usually fell well below the credible interval.

**Table 3**

Grand mean species richness values for the stand age categories, where  $N$  is the number of sites in a given category. Species richness values were derived from the single season, hierarchical multi-species occupancy model.

Category	$N$	Species richness	Standard error
Age 1	8	4.80	0.32
Age 4	8	4.68	0.31
Age 8	7	4.91	0.24
Age 12	8	5.24	0.31
Age 27	5	5.26	0.35
Age 40	6	5.28	0.38

#### 3.2. Occupancy analysis

The seven most commonly caught species were used for the multi-species occupancy model. Average temperature was the most influential detection covariate as determined by the deviance information criterion (DIC, Spiegelhalter et al., 2002). Probability of occupancy for pine voles and short-tailed shrews showed a positive association with elapsed time since harvest, with 95% credible intervals for coefficients failing to include zero (Table 2). Occupancy of short-tailed shrews also was greater at harvest sites with northeast-facing aspects. The incorporation of probability of detection increased mean estimates of occupancy compared to the naïve estimates for all species (Fig. 3).

The incorporation of probability of detection also affected community attributes such as species richness (Table 3). The mean estimated species richness for all sites (5.0) was 39% higher than the naïve mean species richness (3.6). There was a general increase

**Table 4**  
Jaccard's similarity coefficients (95% credible interval) comparing average species richness values between the six different age classes.

	1–2	4–6	8–10	12–16	27–33	>40
Age class						
1–2	1					
4–6	0.75 (0.66, 0.86)	1				
8–10	0.77 (0.67, 0.87)	0.77 (0.68, 0.87)	1			
12–16	0.76 (0.66, 0.87)	0.77 (0.67, 0.87)	0.81 (0.74, 0.90)	1		
27–33	0.74 (0.61, 0.86)	0.76 (0.65, 0.86)	0.82 (0.73, 0.91)	0.82 (0.73, 0.91)	1	
>40	0.74 (0.61, 0.86)	0.76 (0.65, 0.86)	0.81 (0.72, 0.92)	0.82 (0.74, 0.91)	0.85 (0.75, 0.94)	1

**Table 5**  
Results of the single-season, single-species relative abundance analysis for the four most abundant species. Bold-faced type indicates significance ( $p < 0.05$ ).

Parameter	Eastern Chipmunk		Pine vole		Short-tailed shrew		White-footed mouse	
	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE	$\beta_j$	SE
<i>p</i>								
Intercept	-2.03	0.14	-0.76	0.32	-2.66	0.23	-1.95	0.14
JD	<b>0.16</b>	<b>0.04</b>	-	-	<b>-0.40</b>	<b>0.11</b>	-	-
JD <sup>2</sup>	<b>-0.23</b>	<b>0.036</b>	-	-	-	-	-	-
Effort	<b>-0.12</b>	<b>0.041</b>	-	-	-	-	<b>0.20</b>	<b>0.050</b>
Temp	-0.063	0.041	-	-	-	-	-	-
Year	0.32	0.12	-	-	0.43	0.33	0.17	0.15
<i>N</i>								
Intercept	0.94	0.096	-3.99	0.26	-1.36	0.24	0.42	0.093
Age	<b>-0.29</b>	<b>0.059</b>	-	-	-	-	-	-
Aspect	<b>-0.19</b>	<b>0.051</b>	-	-	-	-	-	-
BA	<b>-0.26</b>	<b>0.056</b>	-	-	-	-	<b>0.24</b>	<b>0.039</b>
Canopy	<b>0.18</b>	<b>0.036</b>	-	-	-	-	-	-
CWD	-0.062	0.040	-	-	-	-	<b>0.18</b>	<b>0.057</b>
Gradient	<b>-0.14</b>	<b>0.046</b>	-	-	<b>0.73</b>	<b>0.12</b>	<b>-0.17</b>	<b>0.058</b>
Herb	-	-	0.35	0.20	<b>-0.24</b>	<b>0.094</b>	-	-
Micro CWD	-	-	-	-	-	-	<b>-0.088</b>	<b>0.041</b>
Sapling	-	-	-	-	-	-	-	-
Water	<b>-0.077</b>	<b>0.058</b>	-	-	0.35	0.18	<b>-0.27</b>	<b>0.083</b>

in estimated species richness as the age of site increased but it was not significant ( $F = 2.30$ ,  $p = 0.14$ , d.f. = 40). Mean estimated species richness values were significantly greater in smaller ( $S = 5.3$ ) versus larger ( $S = 4.6$ ) harvest sites ( $t = 2.72$ ,  $p = 0.01$ , d.f. = 40). Sites with southwest-facing aspects ( $S = 5.3$ ) also had significantly higher estimated species richness than sites with northeast-facing aspects ( $S = 4.7$ ,  $t = 2.36$ ,  $p = 0.02$ , d.f. = 40).

Jaccard's similarity coefficients showed a trend of declining similarity with increasing differences in age of cuts (Table 4). Size and aspect dyads shared in common over 3/4 of their species, with similarity values of  $0.779 \pm 0.001$  and  $0.776 \pm 0.001$ , respectively.

### 3.3. Relative abundance

The four most common species were chosen for the relative abundance analysis (Table 5). Probability of detection of eastern chipmunks increased over trapping years ( $p \pm SE$ :  $0.32 \pm 0.119$ ). Paradoxically, increased trapping effort reduced the probability of detection ( $-0.115 \pm 0.0409$ ). JD increased and JD<sup>2</sup> reduced probability of detection, indicating that peak detectability occurred at intermediate dates during the trapping season ( $0.16 \pm 0.04$ ,  $-0.23 \pm 0.04$ ). As Julian day increased, the probability of detection decreased for short-tailed shrews ( $-0.40 \pm 0.11$ ). Increased trapping effort increased the probability of detecting white-footed mice ( $0.20 \pm 0.05$ ).

Significant predictors that negatively influenced abundance of eastern chipmunks were Age, BA, Gradient, and Water (Table 5). Chipmunk abundance was highest at southeast-facing sites. Canopy was the only significant predictor for eastern chipmunks that positively influenced abundance. Increased coarse woody debris, basal area, and gradients at the level of the harvest site increased the abundance of white-footed mice. However, presence of water and increased coarse woody debris at the trap

site decreased the abundance of white-footed mice. Increasingly steep gradients positively influenced short-tailed shrew abundance, whereas increased herbaceous cover decreased abundance.

## 4. Discussion

### 4.1. Probability of detection

Using the hierarchical multi-species occupancy model allowed the inclusion of three shrew species with low capture rates that normally would be excluded from the analysis. All species, especially *Sorex*, were estimated to be much more prevalent than would be inferred solely from capture records. Probability of occupancy estimates increased as much as 74% for southeastern shrews and 79% for pygmy shrews. Even with large credible intervals, the naïve occupancy estimates for white-footed mice, short-tailed shrews, smoky shrews, southeastern shrews, pine voles, and pygmy shrews were below the 2.5% lower credible interval (Fig. 3). The naïve occupancy estimate for eastern chipmunks fell in the lower 27.5% of the posterior distribution. Assuming comparable trappability in other studies suggests that previous estimates of occupancy often have been biased low.

Royle–Nichols estimates of abundance were related to mark-recapture abundance estimates in the two species for which tests could be performed (Fig. 2). Although less desirable than mark-release estimates, the Royle–Nichols method enabled incorporation of detection probability into estimates of relative abundance, a feature lacking from population indexes used previously (Anderson, 2001; Nichols et al., 2000; Thompson et al., 1998). Because marking of individuals was not required, we were able to sample additional sites. Wider spacing of traps likely would have been required to derive absolute estimates of abundance from the Royle–Nichols method in our study. Our results suggest that

future studies focusing on population and community estimates of small mammals can benefit from methods of estimation that account for non-detection error, permit estimates for less common species, and accommodate sampling of a greater number of sites.

#### 4.2. Species responses to environmental covariates

Eastern chipmunk responses to environmental covariates indicated an association with early seral stages, confirming previously documented habitat associations (Schwartz and Schwartz, 2001; Whitaker and Hamilton, 1998). Chipmunks were ubiquitous in occurrence, yet they showed a significant population-level response to forest management. Abundance of chipmunks was negatively related to age of cut and stand basal area, another variable associated with seral stage. Moreover, the magnitude of change was substantial; the predicted relative abundances of chipmunks at “average” young (1–6 years since cut) and old (27+ years since cut) sites differed by 70% (76.3 and 45.0, respectively). Eastern chipmunks are associated with high abundance of seedlings and shallow leaf litter (Kaminski et al., 2007), which are characteristic of early seral stages and disturbance events mimicked by even-aged management. Three years after clearcutting in a Pennsylvania oak forest, eastern chipmunks had increased in abundance, although they maintained home ranges in both harvested and uncut areas (Kirkland et al., 1985). Chipmunks responded similarly to 1–4 year-old clearcuts in northern hardwoods (Lovejoy, 1975). In contrast, chipmunk abundance reportedly declined in response to recent clearcutting of aspen (*Populus* sp.), mixed deciduous–coniferous, and mixed deciduous forests (Probst and Rakstad, 1987; Kirkland, 1977a,b).

White-footed mice were also ubiquitous, and although their populations did not vary with age since harvest, their local populations responded to habitat covariates. Greenburg (2002) found greater capture success for white-footed mice at traps with coarse woody debris. However, trap-level relative abundance in our study was influenced negatively by the amount of coarse woody debris at the individual trap sites. Alternatively, mouse abundance responded positively to coarse woody debris measured at the opening level. We suspect that these scale-dependent responses may result from smaller home ranges and greater travel corridors in sites with considerable coarse woody debris, resulting in fewer individual encounters with traps locally, despite increased abundance at the opening level. Changes in species response to habitat variables at different scales have been documented in both ungulates (reviewed by Bowyer and Kie, 2006) and rodents (Manning and Edge, 2004). Our results further reinforce the importance of including different spatial scales in studies of population responses to management.

Pine voles and short-tailed shrews were more likely to be found in older sites, consistent with their status as later-successional species. Pine voles are associated with habitats containing thick litter and herbaceous cover (Smolen, 1981), corresponding to conditions seen in our study at older sites, where litter accumulated up to 9 cm deep. Previous habitat associations of short-tailed shrews also have noted that deep litter cover is important to protect them from desiccation and high temperatures (Pruitt, 1953, 1959). Short-tailed shrews in our study likewise responded positively to northeast-facing aspects which characterize mesic sites and suggest a dependence on high moisture levels in the litter layer. These two species are likely to respond most negatively in the period shortly following harvest when leaf litter is disturbed and desiccation is most likely. Negative responses to harvest, especially recent clearcuts where litter has recently been disturbed, also were found by Fuller et al. (2004) and Kirkland (1977a,b).

#### 4.3. Community-level responses

Based on the analysis of similarity, communities in older openings tended to be more similar than those in younger openings. Younger openings are rapidly changing from a vegetative standpoint and thus are likely to be more variable in terms of their faunal composition. Lower similarity between younger openings may also result when recolonization following disturbance occurs at varying rates due to landscape-level heterogeneity in connectivity of harvested areas.

Communities of small mammals in our study shifted from chipmunk-dominated assemblages in early successional sites to slightly more diverse mouse-dominated assemblages in older openings. Because of differences in activity periods of dominant species, early successional sites may prove more valuable to diurnal predators, whereas nocturnal predators may benefit more from foraging in older sites. In addition, smaller sites exhibited greater species richness. This is likely due to increased edge effects where more species from the surrounding habitats could “bleed” over into trapping grids at smaller harvest sites. In larger sites, edge effects are minimized, resulting in sampling of the truly “resident” set of species using the harvested area. The difference in species richness shown between sites with northeast- and southwest-facing aspects is more difficult to explain. Our study area receives 114 cm of precipitation annually (NOAA Online Weather Data, <http://weather.gov>, accessed July 2009). Thus, unlike more arid regions, assemblages occupying southwest-facing aspects at NSWC may not be limited by moisture yet may benefit from increased solar radiation, especially during winter months.

Forest management practices at NSWC affected small mammal populations and assemblages. When effects were considered for each site individually, trap- and site-level environmental variables influenced occurrence or abundance of several species. From a community perspective, the cumulative effect of forest management at NSWC provided a mixture of seral stages that elevated the species richness (7.0) above forest stands that had no forest management (5.3).

### 5. Conclusions

There was no effect of harvest area on small mammal occupancy and abundance. The small mammal assemblages of our study responded more to stand structure and microsite characteristics. The small harvest areas were openings caused by uneven-aged group selection methods, whereas larger harvest areas were even-aged clearcuts. The lack of response by any species to the different sized openings caused by these different silvicultural techniques may be due to the relatively large size of the group-selection stands (0.8–1.6 ha). Group selection stands typically range from 0.1 to 0.2 ha but can be >0.2 ha (Johnson et al., 2002). When stands are larger than 0.2 ha, the effects on vegetative structure can be more similar to even-aged management (Johnson et al., 2002).

Although the small mammals on our sites responded primarily to stand structure and microsite characteristics, the types of silvicultural methods used to regenerate oak ultimately may be an important driver of small mammal responses. Moisture retention, varying stand basal areas, reduced herbaceous cover, and canopy cover were important stand characteristics to which the four most abundant species responded. Thus, silvicultural methods that retain some canopy to protect against the drying effects of wind, moderate temperature, and help to retard understory competition (Johnson et al., 2002) can be important to retaining small mammals that otherwise would respond negatively to logging. Even eastern chipmunks, which were associated with xeric, young sites, reacted favorably to percent canopy cover. This

association to closed overstory habitats has been documented previously (Bowers, 1995; Morris, 1979). Silvicultural techniques for oak regeneration that still maintain some canopy cover exist for even-aged (shelterwood, seed tree methods) and uneven-aged systems (single tree, group selection methods) (Johnson et al., 2002). These would be preferable in terms of small mammal assemblages to methods that remove all canopy cover (i.e. clearcuts).

The silvicultural system used to regenerate oak is important for determining whether stands will be managed based on area (even-aged) or in maintaining a stand structure (uneven-aged). However, the small mammal communities on NSWC responded to different forest structures and ages as illustrated by the shift from chipmunk-dominated early successional stands to white-footed mice dominated old successional stands. Landscapes with forest structures of multiple ages and structure can help maintain wildlife diversity (McShea and Healy, 2002). Our study also showed higher diversity in older sites, indicating a need to preserve areas of mature forest. Whether even or uneven-aged management is practiced, small mammals may respond best to a diversity of stand structure across the landscape. However, the importance of spatial arrangement of these different seral types within a landscape is largely unknown with regard to its impact on small mammal meta-communities. Further studies are needed to assess the importance of different forest management practices on small mammal colonization and extinction dynamics at the landscape scale.

Our estimates are among the first to incorporate detection bias into analyses of small mammal responses to forest management, which makes direct comparison to results from earlier studies difficult. The differences in occupancy and abundance estimates relative to naïve estimates were dramatically different, especially for rarer species (Fig. 3). The studies cited previously often used number of individuals (or species) captured, or captures per unit of effort, as population and community response variables, and they often ignored rarer species. Consequently, previous work on small mammal community responses to forest management practices likely provided less accurate estimates than those that incorporate imperfect detection. Forest managers should be aware of these differences when interpreting prior results and developing management plans that include a focus on small mammals.

Of course forest managers may formulate differing goals when considering small mammal communities. Species diversity is not always the sole or even a primary focus of wildlife management. Indeed, species richness may mean little if dynamics of individual species indicate that certain management strategies results in sink habitats. Assessing the abundance of ubiquitous species, such as eastern chipmunks and white-footed mice, can be particularly useful as these rodent species are important acorn consumers (Wolff, 1996; Wolff et al., 1985) and prey for vertebrate predators (Snyder, 1982; Holt, 1997; Whitaker and Hamilton, 1998). The methods in this paper facilitate a more accurate estimate of species richness and make possible the study of rare or elusive species that are often left out of analyses. Our methods also improve accuracy in population estimates for species that could significantly affect the reproductive success of mast-producing tree species and alter forest ecosystems.

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