A PRE-TREATMENT ASSESSMENT OF SMALL MAMMALS IN THE HARDWOOD ECOSYSTEM EXPERIMENT

Natasha A. Urban and Robert K. Swihart[1]

Abstract.—The Hardwood Ecosystem Experiment (HEE) is a 100-year, replicated experiment implemented in south-central Indiana to examine the impacts of multiple timber management regimes on forest ecosystems. A secondary objective of the HEE is to evaluate responses of small mammal assemblages. We trapped at 32 sites prior to silvicultural treatments to assess pre-treatment small mammal communities. Trapping at all sites in both years allowed for modeling of multi-season occupancy and relative abundance using environmental covariates while incorporating imperfect detection. Estimated occupancy probabilities and species richness were larger than naïve estimates. Species richness was not significantly different between treatments or years. Except for the abundance of eastern chipmunks (*Tamias striatus*), the probability of occupancy and relative abundance of species did not differ among proposed treatment units. Abundance of white-footed mice (*Peromyscus leucopus*) and short-tailed shrews (*Blarina brevicauda*) and survival of local populations of pine voles (*Microtus pinetorum*) were greater for sites with northeastern aspects. Abundance of short-tailed shrews and pine voles also increased with greater herbaceous ground cover. By incorporating detection probability, we were able to derive more accurate estimates of relative abundance and, when coupled with a Bayesian framework, estimate occupancy for uncommon species. The baseline responses reported here can be used by forest managers to determine impacts of even-aged and uneven-aged oak (*Quercus*) management on small mammals subsequent to timber harvest.

INTRODUCTION

The most accurate depiction of species responses to forest management involves longitudinal studies that monitor focal taxa at a site from the time of timber harvest until the site is subjected to harvest again. Due to the cost and long-term commitment required of broad-spectrum longitudinal studies, most studies restrict their focus to responses over brief periods before and after a forest management activity (Fantz and Renken 2005, Ford and Rodrigue 2001, Kirkland 1990, Potvin et al. 1999, Yahner 1992) or to responses inferred from chronosequences sampled at a point in time (Urban and Swihart 2011). Although valuable, these short-term studies fail to portray wildlife response to forest regeneration beyond the earliest stages. Further, it is important to observe population dynamics across landscapes, not just within stands (Gram et al. 2001). With the notable exception of the Missouri Ozark Forest Ecosystem Project (MOFEP) (Gram et al. 2001,2003), few studies have been devoted to a complete landscape-level, longitudinal assessment of small mammal responses.

The Hardwood Ecosystem Experiment (HEE) was established in south-central Indiana to examine the ecological and social impacts of alternative forest

[1] Graduate Student (NAU) and Professor (RKS), Purdue University, Department of Forestry and Natural Resources, 715 West State St., West Lafayette, IN 47907; current address of NAU: University of Cincinnati, Department of Biology, Cincinnati, OH 45221. RKS is corresponding author: to contact, call 765-494-3590 or email at rswihart@purdue.edu.

management regimes on public land. Objectives of this 100-year, landscape-level, replicated experiment are reviewed by Kalb and Mycroft (this publication).

Secondary objectives for the HEE include determination of the effect of alternative forest management practices on the long-term distribution, diversity, and abundance of small mammals at local and landscape scales. Within this study, we sought to characterize the small mammal communities and populations of the HEE forest stands before silvicultural treatments were applied.

STUDY AREA

Sampling sites were located in three different publicly owned tracts, all located in the Brown County Hills region between Bloomington, Martinsville, and Nashville, IN. Two of the tracts, Morgan-Monroe State Forest (MMSF) and Yellowwood State Forest (YWSF), are part of the HEE and are discussed in more detail by Kalb and Mycroft (this publication). The third location, Brown County State Park (BCSP), was established in 1920 and is the largest state park in Indiana at 64 km^2 (lat. 39°16' N long. 86°22' W). All three sites have a similar history inasmuch as they all consist of land that was farmed in the 1800s and early 1900s and then reverted to stands of native oak-hickory (*Quercus-Carya*), American beech-maple (*Fagus grandifolia-Acer*), and mixed mesophytic forest with scattered pine (*Pinus*) plantations established in the early half of the 20th century (Carman, this publication). BCSP has not been subjected to timber harvest since its inception, whereas the State Forests have been harvested, principally via uneven-aged management, over the past several decades.[2] Sample site selection and descriptions for MMSF and YWSF are described by Kalb and Mycroft (this publication). Four small-mammal trapping grids were established in each of the 6 treatment research cores, resulting in 12 grids per management treatment (Fig. 1). Along with the three HEE control trapping sites at MMSF and YWSF, a fourth was located in BCSP. Two trapping grids were established at each of the four sampling sites, resulting in a total of eight control grids for sampling of small mammals (Fig. 1).

MATERIALS AND METHODS

Mammal Sampling

Each grid consisted of 27 trapping stations arranged in a 3 x 9 lattice (Fig. 2). The three long transect lines were laid out 50 m apart across the slope with 20- to 50-m spacing between stations, depending on the size of the harvest treatment (Figs. 2a,b). As with the

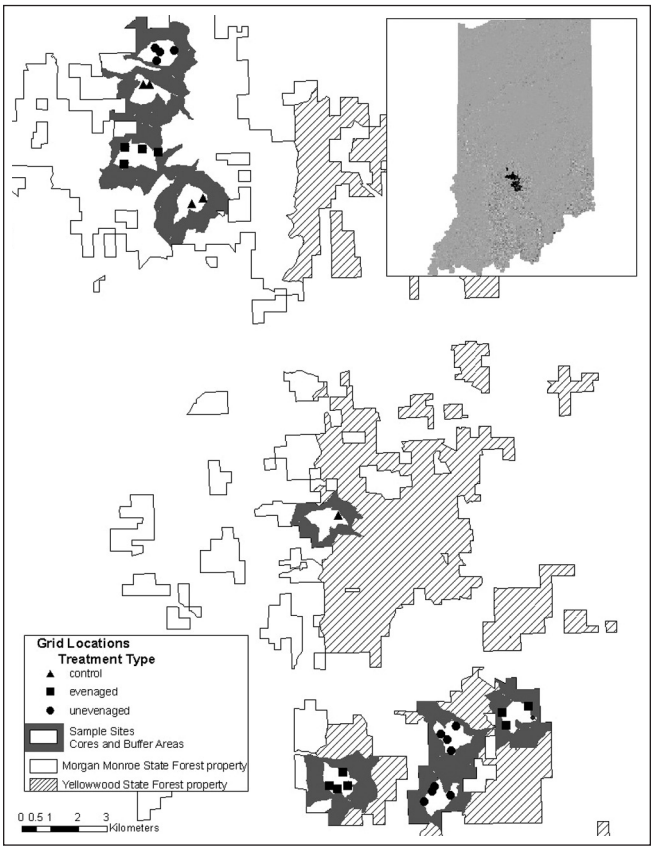

Figure 1.—Sampling sites and small mammal grid locations for the Hardwood Ecosystem Experiment. These nine sampling sites are located in Morgan-Monroe and Yellowwood State Forests. A tenth sampling site is located at Brown County State Park and contains a control grid.

[2] Duane McCoy, Indiana Department of Natural Resources-Division of Forestry, and Mike Mycroft, Indiana Department of Natural Resources-Division of State Parks and Reservoirs, personal communication

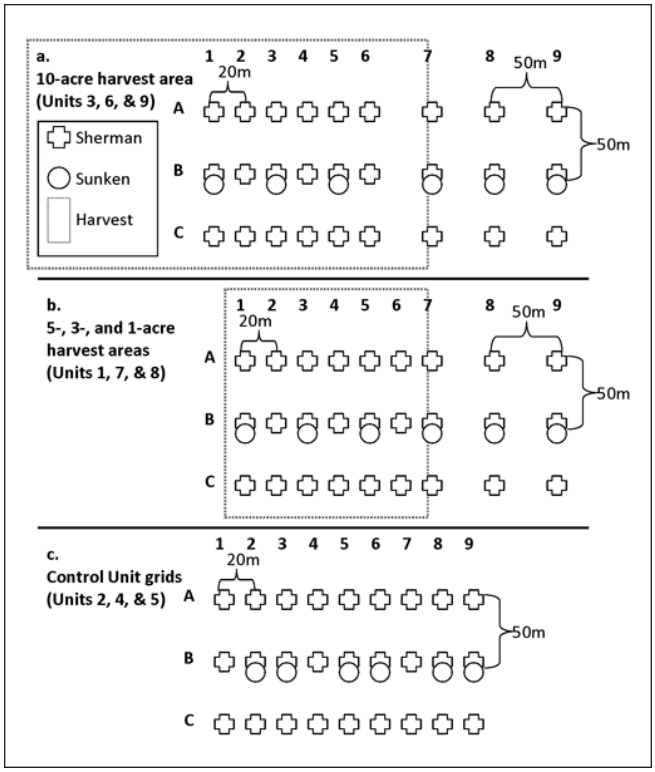

Figure 2.—Layout of Hardwood Ecosystem Experiment small mammal trapping grids. Several grid orientations were used depending on the size and treatment of the potential harvest area.

treatment grids, the control grids contained 27 stations allocated among three transects that were spaced 50 meters from each other and were placed across slope (Fig. 2c).

Every station received a Sherman trap (H.B. Sherman Trap, Inc., Tallahassee FL), and six sunken traps were placed within the harvest area on the center transect (Fig. 2). The sunken traps were composed of 16.5cm x 15.9cm aluminum cans with small perforations for drainage. Sherman and sunken traps were placed within 1 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 to discourage their immediate return to the site.

Sherman traps were pre-baited for the 3 days preceding 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. All trapping and handling procedures were approved by the Purdue Animal Care and Use Committee (protocol #07-045).

Vegetation Sampling

For each harvest site, a short site description was recorded. 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 (d.b.h.) were identified to species and d.b.h. was 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, an ocular estimate of cover of herbaceous plants and seedlings <1 m tall was made within a 1-m^2 quadrat. All saplings <5 cm d.b.h. 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 up slope, down slope, and perpendicular to slopes from the center of each harvest area. At each sampling point, a density pole was used to measure vegetation density in four vertical strata with 1-m height increments. At each decimeter on the density pole, vegetation within 5 cm of the pole was counted as a contact, 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.

Analysis Based on Occurrence

All sites were sampled for 2 consecutive years, thus permitting use of a multi-season, Bayesian hierarchical multi-species model of site occupancy that incorporated imperfect detection (Kéry and Royle 2008, Royle and Dorazio 2008: 390-393). The model enables estimation of both species- and community-level attributes, including survival and colonization parameters.

The general structure of the hierarchical model has been described in detail elsewhere (e.g., Royle and Dorazio 2008). Briefly, each of *R* (=32) harvest sites is visited on *J* (=5) occasions for *T* (=2) years, and for each occasion a record is made of species detected. For each of the *n* species, a count, y_{kt}, denotes the number of detections of the species in *J* visits to site *k* in year *t*. Conditional on the target species' occurrence at site *k*, the corresponding y_{kt} can be modeled as a binomial random variable with *J* trials consisting of detection probability p_{kt}. The detection frequencies for each of the *i*th observed species at the *R* sites can be summarized conveniently in a matrix $\mathbf{Y}_{n*R}$. For the initial year (*t*=1) and for the *i*th species and *k*th site, the species occurs with probability ψ_{ik}. A latent state variable z_{ikt} represents whether the species occurs at the site (z_{ikt}=1) or not (z_{ikt}=0). Occupancy state of the subsequent year (*t*+1) and survival ($\varnothing_t$) and colonization (γ_t) probabilities are dependent on the initial occupancy state (Royle and Dorazio 2008):

$$z(i,k,t+1) \mid z(i,k,t) = \text{Bernoulli}(\pi(i,t))$$

where

$$\pi(i,t) = z(i,k,t)(\varnothing_i)+[1 - z(i,k,t)]y_i .$$

In words, the occupancy state for species *i* at site *k* in year *t*+1 is treated as a Bernoulli random variable that is conditioned on the prior year's occupancy state. If the site was occupied by the species in year *t*, the probability of occupancy in *t*+1 is determined by the probability of survival from *t* to *t*+1. But if the site was unoccupied in year *t*, its probability of occupancy is determined by the probability of colonization during the period *t* to *t*+1. Thus, the hierarchical model includes a matrix $\mathbf{Z}_{ikt}$ of state variables that are only partially observed because 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. Occurrence and detection were modeled as hyperparameters. Specifically, we defined u_i = logit(ψ_{ik}) and v_i = logit(p_{ik}), where logit(*x*) = ln(x/(1-x)). Interspecific heterogeneity in ψ and *p* were modeled with bivariate normal distributions, i.e., $u_i \sim N(\beta,\sigma_u^2)$, $v_i \sim N(\alpha, \sigma_v^2)$, and covariance σ_{uv}. The parameters β and α 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: 382).

The hierarchical model is easily extended to incorporate effects of environmental covariates on ψ_{ikt}, the probability of occurrence of species *i* at site *k* in year *t*. Using the notation above, $z_{ikt} \mid \psi_{ikt} \sim$Bernoulli($\psi_{ikt}$), where logit($\psi_{ikt}$) is a linear function of site-specific covariates. Planned treatment type,

basal area, and aspect were chosen as site covariates of occurrence. Incorporating covariates into the observation portion of the model required modified notation because detection may differ among species, sites, sampling occasions, and years. Thus, y_{ijkt} is a binary observation indicating detection (y_{ijkt}=1) or not (y_{ijkt}=0) of species *i* during the *j*th visit to site *k* in the *t*th year. Then $y_{ijkt}|p_{ijkt},z_{ikt}$~Bernoulli($p_{ijkt},z_{ikt}$), where logit($p_{ijkt}$) is a linear function of site- or time-specific covariates that could influence detection. We considered average daily temperature (Temp), precipitation (Precip), year, sampling effort (Effort), Julian day (JD), and squared Julian day centered around the mean (JD^2) as possible covariates of detection. Detection covariate data are summarized in Appendix 1. We determined the best combination of detection covariates with the smallest deviance information criterion (DIC) value (Spiegelhalter et al. 2002). We then incorporated the chosen site-specific occupancy covariates: even-aged treatment type (Trt 1), uneven-aged treatment type (Trt 2), aspect, and basal area (BA). Management treatment types were grouped according to management system: even-aged or uneven-aged. All continuous occupancy and detection covariates were standardized prior to analysis.

The multi-season hierarchical multi-species site-occupancy model was implemented within a Bayesian framework (Appendix 2). 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 α and β from uniform distributions over the interval [0, 1], priors for σ_u and σ_v from uniform [0, 10], and priors for the correlation of *u* and *v*, $\rho=\sigma_{uv}/\sigma_u\sigma_v$, from uniform [-1, 1]. The model was implemented in the software package R 2.6.1 (R Development Core Team, Vienna, Austria) using the add-on package R2WinBUGS (Sturtz et al. 2005), which calls the software package WinBUGS (version 1.4.3; Lunn et al. 2000, Spiegelhalter et al. 1996). WinBUGS uses Markov chain Monte Carlo techniques to derive posterior distributions for model parameters.

For each run, we used five parallel chains of length 55,000 and discarded the first 5,000 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 $s_k = \sum_{i=1}^{n} z_{ikt}$. An estimate of average species richness for 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., $\overline{S}_a = \sum_{k \in a} S_k / A$. Estimates of average species richness were thus obtained for each potential treatment type of harvest sites. The same procedure was used to derive estimates of the average similarity between pairs of categories for each year. We used Jaccard's coefficient (Jaccard 1912) to measure similarity in species richness between categories a and b:

$$C_{ab} = \frac{S_{a \cap b}}{S_a + S_b - S_{a \cap b}}$$

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

Analysis Based on Relative Abundance

For the four most commonly captured species, we implemented a multi-season version of the Royle and Nichols (2003) model, incorporating heterogeneity in *p* with finite mixtures. For N_{kt} animals at trap location *k*, replicate sampling yields a record of the number of animals detected there for each year *t*. Then the probability of detecting at least one animal at the location, given that the species occurs there, is $p_{kt} = 1-(1-r)^{N_{kt}}$, where *r* is the probability of capturing an individual (Royle and Nichols 2003).

Considering abundance as a Poisson random variable, i.e., $Pr(N\text{-}n)=e^{-\lambda}\lambda^{n}/n!$ where λ is the mean of the Poisson distribution on *N*, permits estimation of *r* and λ by the method of maximum likelihood (Royle and Nichols 2003).

We implemented a multi-season version of the Royle-Nichols model using PRESENCE 2.4 (Hines 2006) with species-level detection histories developed for each trap location. Because a single detection model is fitted to observations from all harvest sites, site-specific estimates of density are not independent. Thus, we used the two-stage bootstrap method of Buckland et al. (2009) to quantify precision. Specifically, 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 λ and chose the model with the lowest AIC.

Detection covariates considered for analysis were JD, JD^2, year, Effort, Temp, and Precip. Site-specific covariates for λ were coarse woody debris at the trap level (Micro CWD), percentage of herbaceous cover at the trap level (Herb), percentage of woody cover at the trap level (Wood), depth of leaf litter at trap level (Litter), Trt 1, Trt 2, BA, and aspect. Confidence intervals and standard errors for each parameter were estimated using bootstrap re-sampling of trap locations in each harvest site (Urban 2010). The selected Royle and Nichols (2003) model was fitted in R 2.6.1 using at least 200 bootstrap samples for each species, resulting in 200 x 1,728 trap-specific abundance values. These estimates were used to derive standard errors of N for each harvest site. Trap spacing was likely to result in multiple trap stations within a home range, so we suspect that our estimates of λ are biased high and are more likely to serve as estimates of relative abundance (Urban and Swihart 2011).

RESULTS

Trapping Results

Trapping in 2007 occurred from 25 June through 3 August with 8,936 trap nights and 6 species captured. In 2008 trapping took place from 16 June to 25 July for a total of 8,978 trap nights and 7 species captured. Total captures consisted of 2,101 white-footed mice (see Table 1 for list of common and scientific names), 1,143 eastern chipmunks, 96 pine voles, 71 short-tailed shrews, 4 smoky shrews, 4 southeastern shrews, and 3 long-tailed weasels.

Occupancy Analysis

All species were used for the multi-season, multi-species occupancy models. Average temperature and Julian day were the best DIC detection covariates for both years of data. Pine voles were more detectable during later trapping dates (Table 2). Conversely, eastern chipmunks had higher detections during earlier trapping dates. Mean estimates of occupancy for all species and for both years increased from naïve occupancy after the incorporation of detection probability (Fig. 3). Ninety-five-percent credible intervals for all treatment covariate by species combinations contained zero, indicating that they were not useful predictors of occupancy for any of the seven species. Likewise, treatment did not affect the survival or colonization of local populations, with one exception (Table 3). Survival of local pine vole populations was positively affected by northeastern aspects.

The incorporation of probability of detection increased species richness values. The mean estimated species richness for all sites in 2007 (4.6) was 47 percent higher than the naïve mean species richness (3.1). In 2008, the mean estimated species richness (4.8) was 60 percent higher than naïve richness (3.0). Mean estimated species richness did not differ significantly among treatment types ($F = 0.47$, $p = 0.63$) or years ($F = 0.60$, $p = 0.44$).

Table 1.—Trapping results for the Hardwood Ecosystem Experiment pre-treatment sampling period. Seven species were captured during the 2007 and 2008 sampling period. All seven species were used for the occupancy analysis, and the four most common were used for the relative abundance analysis.

Species	Scientific name	2007	2008	Total
White-footed mouse	*Peromyscus leucopus*	1,152	949	2,101
Eastern chipmunk	*Tamias striatus*	453	690	1,143
Pine vole	*Microtus pinetorum*	47	49	96
Short-tailed shrew	*Blarina brevicauda*	39	32	71
Smoky shrew	*Sorex fumeus*	3	1	4
Southeastern shrew	*Sorex longirostris*	3	1	4
Long-tailed weasel	*Mustela frenata*	0	3	3

Table 2.—Results from the multi-season, hierarchical multi-species occupancy model analyzed within a Bayesian framework. Asterisk (*) indicates parameters for which 95-percent credible intervals excluded zero.

	White-footed mouse	Eastern chipmunk	Pine vole	Short-tailed shrew	Smoky shrew	Southeastern shrew	Long-tailed weasel
Covariate	β_i SE	β_i SE	β_i SE	β_i SE	β_i SE	β_i SE	β_i SE
p	-0.02	-0.29*	0.39*	-0.10	-0.49	-0.68	0.19
Julian day	0.14	0.17*	0.21*	0.20	0.47	0.52	0.45
	-0.04	-0.07	-0.13	0.06	-0.01	0.02	0.00
Temperature	0.12	0.14	0.16	0.17	0.22	0.23	0.24
Ψ	0.98	0.38	0.36	0.91	1.18	0.16	0.18
Uneven-aged	1.31	1.10	0.94	1.26	1.42	1.57	1.54
	0.78	-0.01	0.35	-0.85	-0.74	1.22	-0.52
Even-aged	1.50	1.18	1.05	1.27	1.83	1.67	1.68
	-0.14	-0.24	-0.12	-0.09	-0.38	-0.12	-0.10
Basal area	0.61	0.50	0.38	0.47	0.75	0.87	0.80
	0.97	-0.32	1.04	0.73	0.49	0.45	0.00
Aspect	1.30	1.13	0.91	1.10	1.46	1.48	1.53

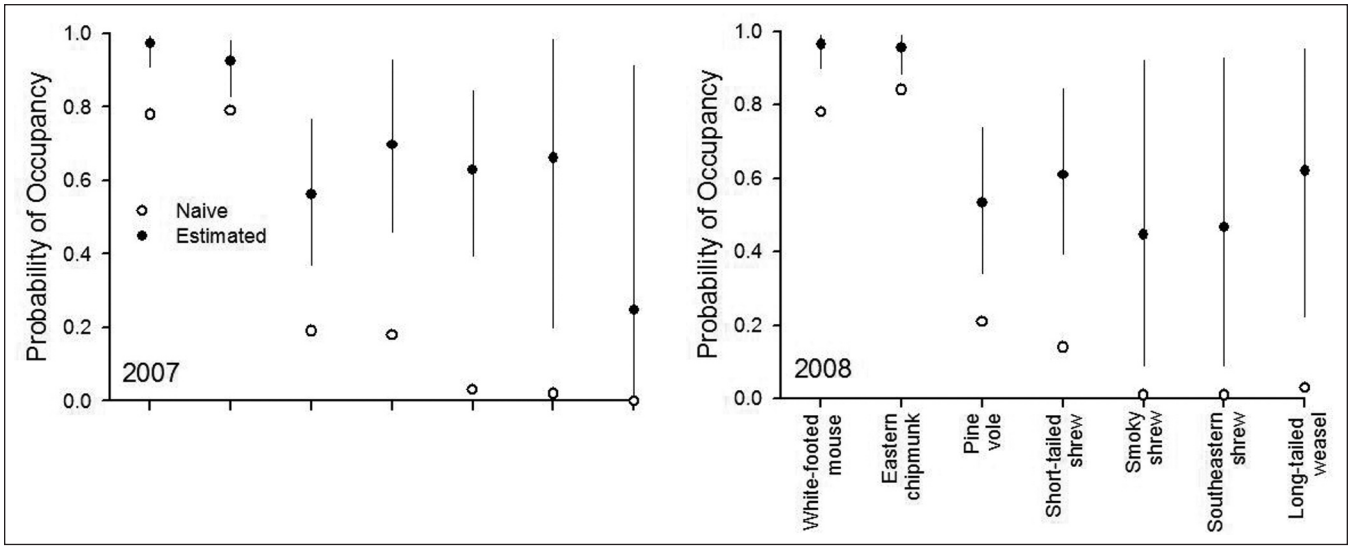

Figure 3.—Naïve and estimated (95-percent credible interval) values for probability of occupancy from the multi-season, multi-species occupancy model. All estimated occupancy values were higher than the naïve values.

Table 3.—Survival and colonization parameters from the multi-season, hierarchical multi-species occupancy model analyzed within a Bayesian framework. Models included even-aged or uneven-aged proposed treatment type, aspect, and basal area occupancy covariates as explanatory variables. The best detection probability covariates included were Julian day and average temperature, as determined by the lowest Deviance Information Criterion. Asterisk (*) indicates parameters for which 95-percent credible intervals excluded zero.

	White-footed mouse	Eastern chipmunk	Pine vole	Short-tailed shrew	Smoky shrew	Southeastern shrew	Long-tailed weasel
Covariate	β_j SE	β_j SE	β_j SE	β_j SE	β_j SE	β_j SE	β_j SE
Uneven-aged							
Colonization	0.52	0.88	1.22	0.60	0.32	0.44	0.43
	1.95	1.79	1.67	1.87	1.98	1.92	2.00
Survival	1.25	1.22	0.75	1.18	0.16	0.69	0.74
	1.45	1.47	1.46	1.43	1.89	1.73	1.76
Even-aged							
Colonization	-0.96	-0.45	-1.71	-1.35	-1.23	-1.04	-1.45
	1.96	1.90	1.49	1.63	1.88	1.91	1.87
Survival	1.17	1.17	1.13	0.63	0.52	0.45	0.64
	1.44	1.45	1.34	1.57	1.80	1.81	1.78
Basal area							
Colonization	-0.09	0.37	0.59	-1.09	-0.19	-0.50	-0.01
	1.88	1.86	1.50	1.74	1.86	1.84	1.60
Survival	-0.09	-0.09	-0.23	0.02	-0.03	-0.29	-0.06
	0.83	0.84	0.88	0.71	1.16	1.16	1.19
Aspect							
Colonization	0.15	1.13	-0.34	0.31	-0.19	-0.16	0.40
	1.99	1.77	1.66	1.66	1.97	1.99	1.82
Survival	1.85	1.82	2.26*	1.99	0.74	0.80	1.36
	1.44	1.47	1.29*	1.37	2.10	2.07	1.86

Jaccard's similarity coefficients for 2007 and 2008 indicated that all pairs of projected treatments had nearly two-thirds of their species in common (Table 4). This level of similarity was consistent across years.

Relative Abundance Analysis

White-footed mice, eastern chipmunks, pine voles, and short-tailed shrews were captured in sufficient numbers for the multi-season, single-species relative abundance analysis. All species except pine voles were more detectable during earlier trapping (Table 5). Trapping effort positively influenced probability of detection of mice and pine voles. Increased trapping effort and occurrence of precipitation negatively influenced eastern chipmunk detection probability, whereas increased temperature positively influenced detection probability. Occurrence of precipitation also negatively affected white-footed mice.

Relative abundance of white-footed mice and short-tailed shrews was greater on sites with northeastern aspects versus southwestern aspects. Short-tailed shrew and pine vole relative abundance was greater on sites with increased herbaceous cover. Pine voles also had higher relative abundance with greater amounts of coarse woody debris at the trap level. Relative abundance of eastern chipmunks was lower on sites proposed for even-aged treatment.

Table 4.—Jaccard's similarity coefficients (95-percent credible interval) comparing species richness values between the different proposed treatment types. Comparisons were made for each year separately. A similarity coefficient value of 1 indicates total overlap in species, whereas a value of 0 indicates no shared species. Comparisons for 2007 are located above the diagonal and comparisons for 2008 are below.

Treatment type	Treatment type		
	Even-aged	Uneven-aged	Control
Even-aged	1	0.61 (0.54, 0.76)	0.63 (0.55, 0.77)
Uneven-aged	0.61 (0.55, 0.76)	1	0.62 (0.56, 0.76)
Control	0.63 (0.55, 0.78)	0.63 (0.55, 0.77)	1

Table 5.—Results for the multiple-season, single-species relative abundance analysis for the four most abundant species. Bold-faced type indicates significance (P < 0.05). Asterisk (*) indicates parameters for which 95-percent credible intervals excluded zero.

Parameter	White-footed mouse		Eastern chipmunk		Pine vole		Short-tailed shrew	
Covariate	β_j	SE	β_j	SE	β_j	SE	β_j	SE
p								
Intercept	-1.75*	0.12*	-1.61*	0.41*	-2.55*	0.46*	-2.40*	0.48*
Julian day	-0.73*	0.12*	-0.39*	0.17*			-1.53*	0.77*
Julian day^2			0.06	0.10	0.64	0.46		
Trapping effort	0.59*	0.12*	-0.55*	0.12*	1.49*	0.57*	0.02	0.28
Temperature			0.58*	0.11*				
Precipitation	-1.17*	0.12*	-0.38*	0.13*			-0.28	0.60
N								
Intercept	0.27*	0.11*	0.10	0.14	-2.96*	0.34*	-4.32*	0.66*
Uneven-aged								
Even-aged	-0.15	0.10	-0.82*	0.14*				
Aspect	0.38*	0.09*	0.18	0.10	0.51	0.37	1.62*	0.63*
Basal area							0.81	0.42
Herb					0.31*	0.15*	1.62*	0.63*
Wood			0.11	0.05				
Micro CWD							0.42*	0.21*

DISCUSSION

Probability of Detection

The incorporation of probability of detection increased occupancy probabilities for all species in 2007 and 2008 relative to naïve estimates. Large credible intervals characterized the occupancy analysis, but naïve estimates for all species in both years were still smaller than the 2.5-percent lower credible intervals. Larger credible intervals and elevated occupancy probabilities were produced for the rarer species due to their lower estimated probabilities of detection. Occupancy estimates for species with a probability of detection less than 0.15 should be viewed with caution when sampling occasions are less than seven, as models may not properly distinguish between a truly absent species and a non-detection (MacKenzie et al. 2002). Researchers conducting small mammal studies at our sampling sites may wish to follow minimum sampling guidelines developed by MacKenzie et al. (2002) to better estimate minimum number of sites based on detection probabilities and number of sampling occasions.

Treatment Effects

The planned forest management practices for the HEE have the potential to alter small mammal populations and assemblages. Our study revealed few pre-harvest differences among the sites chosen for the various treatments. Especially encouraging to future small mammal work on the HEE, treatment type was not a significant predictor of probability of occupancy or abundance, except for lower relative abundance of eastern chipmunks on sites slated for even-aged management. Species richness and similarity also did not differ greatly among treatment types. These similar pre-treatment levels will enable easier interpretations of treatment effects in subsequent analyses.

Site descriptors of forest structure, basal area, and aspect failed to influence probability of occupancy for most species. One exception was higher survival of pine vole populations occupying northeastern aspects. For most species relative abundance was affected by site descriptors of forest structure and aspect. Abundance of white-footed mice and short-tailed shrews was higher on northeastern facing sites, which are often cooler and more mesic. Along with showing a relationship with northeastern aspect, short-tailed shrews were found on sites with increased herbaceous cover and trap-level coarse woody debris. Pine voles also were more abundant with increased herbaceous cover.

Similar reactions from these species have been documented in multiple studies. Higher occupancy probability has been seen for short-tailed shrews on northeastern sites in south-central Indiana (Urban and Swihart 2011). Miller and Getz (1977) also found that short-tailed shrews were more common at New England sites with higher herbaceous cover. Pine voles are associated with habitats containing thick litter and herbaceous cover (Smolen 1981).

Previous habitat studies of short-tailed shrews in Michigan noted that deep litter cover is important to protect them from dessication and high temperatures (Pruitt 1953, 1959). Getz (1961) concluded that short-tailed shrews avoid areas with little vegetative cover and extreme temperatures and moisture levels in Illinois. Schmid-Holmes and Drickamer (2001) reported higher abundance for short-tailed shrews at Illinois sites with less extreme temperature fluctuations and higher tree densities, indicative of older seral stages.

The relationships between these species and increased herbaceous cover, coarse woody debris, and northeastern aspects indicate that they may have an initial negative response to proposed forest management treatments. Schmid-Holmes and Drickamer (2001) found greater abundance of white-footed mice in older forests that were subjected to no harvest or uneven-aged harvesting. A shift from young post-harvest openings of small mammal assemblages dominated by eastern chipmunks to old harvest sites dominated by white-footed mice occurred along a chronosequence in south-central Indiana (Urban and Swihart 2011). Pine voles and short-tailed shrews also were more likely to be found in older sites along the chronosequence. However, other studies have indicated that both even-aged and uneven-aged management may positively influence *Peromyscus* abundance, and short-tailed shrews may have no change in abundance (Fantz and Renken 2005, Ford and Rodrigue 2001).

Community-Level Responses

Our pre-treatment analysis described the baseline community structure and population dynamics for the HEE. Subsequent studies should use analytical methods similar to the ones described in this chapter in order to accurately describe and compare post- and pre-treatment data. However, we suggest that a more intensive sampling scheme should be used to increase captures of less common species. Increased trapping effort and subsequent higher captures of rare and elusive species could improve future analyses

using multi-season, multi-species occupancy models. Specifically, focusing trapping effort to sample existing sites more often instead of surveying an increased number of sites less often likely would improve the precision of these occupancy estimates (MacKenzie and Royle 2005).

If detection probabilities remain low, a removal sampling design may produce more precise estimates (MacKenzie and Royle 2005). Increased capture rates would help reduce the large credible intervals associated with *Sorex* occupancy estimates. Increased capture rates also could allow more precise estimation of extinction and colonization rates between post- and pre-treatment data, which could be informative in understanding treatment effects.

Potential Effects of Oak Management

Results from a chronosequence in similar habitat with similar management practices can provide an idea of what changes to expect in the HEE small mammal community following treatment. Based on our analysis of a chronosequence at Crane Naval Surface Warfare Center (NSWC) in 2007 and 2008 (Urban and Swihart 2011), we offer the following predictions for responses of small mammals to the HEE treatments.

The most frequently captured species at the HEE was the white-footed mouse, which was ubiquitous but most strongly associated with older seral stages found at NSWC sample sites. In contrast, the eastern chipmunk was the most frequently captured species on NSWC, where forest management practices have been ongoing since the 1950s. The early successional openings at NSWC were dominated primarily by eastern chipmunks. In general, NSWC was characterized by a shift from chipmunk-dominated early successional openings to more diverse white-footed mouse-dominated late-successional openings. Pine voles and short-tailed shrews also were associated with older sites at NSWC. Thus, we predict increases in eastern chipmunks on recently harvested even-aged and uneven-aged stands. In contrast, white-footed mice, shrews, and pine voles, and hence species richness, should decrease at these early successional sites. As stands mature, a reversal of these trends is likely to occur.

Short-tailed shrews were positively associated with northeastern aspects at both NWSC and the HEE, whereas white-footed mice were positively associated with northeastern aspects at the HEE and eastern chipmunks were negatively associated with this aspect at NSWC. *Blarina* and *Sorex* are sensitive to dry environments (Brannon 2002; Getz 1961; McShea et al. 2003; Pruitt 1953, 1959); hence, we predict increases in shrews on northeastern aspects, especially as successional changes lead to increased litter layer development. Eastern chipmunks should be most prevalent at drier early successional sites. No effect of opening size created by even-aged and uneven-aged harvesting was found on small mammal populations at NSWC sites, although species richness was greater at smaller openings. Consequently, we predict that small mammal populations at the HEE will not respond to the size of harvest openings, although species richness may increase at smaller sites as an artifact of sampling species associated primarily with adjacent habitats.

White-footed mice at NSWC exhibited greater relative abundance in openings with high levels of basal area and coarse woody debris. In contrast, eastern chipmunks at NSWC exhibited greater relative abundance in openings with low basal area and high canopy closure. Based on these results, we predict that white-footed mice will be more abundant in sites with greater tree retention and where coarse woody debris has been retained. These conditions could occur in more mature stands, greater than 27 years, or in harvest areas that remove fewer trees.

Eastern chipmunks should have larger numbers at young sites that still retain some canopy cover, such as 4- to 12-year-old sites. They should also

have greater numbers at sites with more intensive harvesting techniques that retain some canopy cover, such as shelterwood, seed tree, and group selection methods. However, these species are likely to have varying numbers within a site as well. White-footed mice likely will exhibit higher abundance around coarse woody debris or patches of trees within a site. At NSWC, relative abundance of chipmunks and mice was negatively affected by proximity to water, whereas the opposite was true for short-tailed shrews. Following harvest, we predict that these associations will emerge at the HEE sites.

We did not consider the importance of mast to the population dynamics of the small mammal assemblages at the HEE. The two dominant species in the small mammal system at the HEE, white-footed mice and eastern chipmunks, are important mast consumers whose abundances are affected by mast production (McShea 2000, Wolff 1996). The amount of oak basal area, oak as a percent of the total basal area, and mast production data may explain spatial or temporal variation in abundance of these species. These data are currently being collected at our study sites (Kellner et al., this publication).

ACKNOWLEDGMENTS

This paper is a contribution of the Hardwood Ecosystem Experiment, a partnership of the Indiana Department of Natural Resources (IDNR), Purdue University, Ball State University, Indiana State University, Drake University, Indiana University of Pennsylvania, and The Nature Conservancy. Funding for the project was provided by the IDNR-Division of Forestry and Purdue University, Department of Forestry and Natural Resources. We would like to thank the numerous technicians who assisted with trapping and collection of vegetation data. Michael R. Saunders, G. Scott Haulton, John B. Dunning, Nate Lichti, Byju Govindan, Ken Kellner, and Harmony Dalgleish provided helpful suggestions that improved the manuscript. Cortney Mycroft and Rebecca Kalb provided technical and logistical assistance.

LITERATURE CITED

Brannon, M.P. 2002. **Distribution of *Sorex cinereus* and *S. fumeus* on north- and south-facing slopes in the southern Appalachian Mountains.** Southeastern Naturalist. 1(3): 299-306.

Brooks, S.P.; Gelman, A. 1998. **General methods for monitoring convergence of iterative simulations.** Journal of Computational and Graphical Statistics. 7(4): 424-455.

Buckland, S.T.; Russell, R.E.; Dickson, B.G.; Saab, V.A.; Gorman, D.N.; Block, W.M. 2009. **Analyzing designed experiments in distance sampling.** Journal of Agricultural Biological and Environmental Statistics. 14(4): 432-442.

Burnham, K.P.; Anderson, D.R. 2002. **Model selection and multimodel inference: a practical information-theoretic approach.** 2nd ed. New York: Springer-Verlag. 488 p.

Fantz, D.K.; Renken, R.B. 2005. **Short-term landscape-scale effects of forest management of *Peromyscus* spp. mice within Missouri Ozark forests.** Wildlife Society Bulletin. 33(1): 293-301.

Ford, W.M.; Rodrigue, J.L. 2001. **Soricid abundance in partial overstory removal harvests and riparian areas in an industrial forest landscape of the central Appalachians.** Forest Ecology and Management. 152(11): 159-168.

Getz, L.L. 1961. **Factors influencing the local distribution of shrews.** The American Midland Naturalist. 65(1): 67-88.

Gram, W.K.; Sork, V.L.; Marquis, R.J.; Renken, R.B.; Clawson, R.L.; Faaborg, J.; Fantz, D.K.; Le Corff, J.; Lill, J.; Porneluzi, P.A. 2001. **Evaluating the effects of ecosystem management: a case study in a Missouri Ozark forest.** Ecological Applications. 11(6): 1667-1679.

Gram, W.K.; Porneluzi, P.A.; Clawson, R.L.; Faaborg, J.; Richter, S.C. 2003. **Effects of experimental forest management on density and nesting success of bird species in Missouri Ozark forests.** Conservation Biology. 17(7): 1324-1337.

Hines, J.E. 2006. **PRESENCE2 - software to estimate patch occupancy and related parameters.** Available: USGS-PWRC: http://www.mbr-pwrc.usgs.gov/software/presence.html. (Accessed 5 October 2012).

Jaccard, P. 1912. **The distribution of the flora in the alpine zone.** The New Phytologist. 11(2): 37-50.

Kéry, M.; Royle, J.A. 2008. **Hierarchical Bayes estimation of species richness and occupancy in spatially replicated surveys.** Journal of Applied Ecology. 45(2): 589-598.

Kirkland, G.L. 1990. **Patterns of initial small mammal community change after clearcutting of temperate North American forests.** Oikos. 59(3): 313-320.

Lunn, D.J.; Thomas, A.; Best, N.; Spiegelhalter, D. 2000. **WinBUGS -- a Bayesian modelling framework: concepts, structure, and extensibility.** Statistics and Computing. 10(4): 325-337.

MacKenzie, D.I.; Nichols, J.D.; Lachman, G.B.; Droege, S.; Royle, J.A.; Langtimm, C.A. 2002. **Estimating site occupancy rates when detection probabilities are less than one.** Ecology. 83(8): 2248-2255.

MacKenzie, D.I.; Royle, J.A. 2005. **Designing occupancy studies: general advice and allocating survey effort.** Journal of Applied Ecology. 42(6): 1105-1114.

Maser, C.; Anderson, R.G.; Cromack, K., Jr.; Williams, J.T.; Martin, R.E. 1979. **Dead and down woody material.** In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handbk. 553. Washington, DC: U.S. Department of Agriculture, Forest Service, North Central Forest Experiment Station: 78-95.

McShea, W.J. 2000. **The influence of acorn crops on annual variation in rodent and bird populations.** Ecology. 81(1): 228-238.

McShea, W.J.; Pagels, J.; Orrock, J.; Harper, E.; Koy, K. 2003. **Mesic deciduous forest as patches of small-mammal richness within an Appalachian Mountain forest.** Journal of Mammalogy. 84(2): 627-643.

Miller, D.H.; Getz, L.L. 1977. **Factors influencing local distribution and species diversity of forest small mammals in New England.** Canadian Journal of Zoology. 55(5): 806-814.

Mills, G.S.; Dunning, J.B., Jr.; Bates, J.M. 1991. **The relationship between breeding bird density and vegetation volume.** Wilson Bulletin. 103(3): 468-469.

Ntzoufras, I. 2009. **Bayesian modeling using WinBUGS.** Hoboken, NJ: John Wiley and Sons, Inc. 38 p.

Potvin, F.; Courtois, R.; Belanger, L. 1999. **Short-term response of wildlife to clear-cutting in Quebec boreal forest: multiscale effects and management implications.** Canadian Journal of Forest Research. 29(7): 1120-1127.

Pruitt, W.O. 1953. **An analysis of some physical factors affecting the local distribution of the short-tail shrew (*Blarina brevicauda*) in the northeast part of the lower peninsula of Michigan.** Ann Arbor, MI: Museum of Zoology, University of Michigan Press. 79: 1-39.

Pruitt, W.O. 1959. **Microclimates and local distribution of small mammals on the George Reserve, Michigan.** Ann Arbor, MI: Museum of Zoology, University of Michigan Press. 109: 1-27.

Royle, J.A.; Dorazio, R.M. 2008. **Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities.** San Diego, CA: Elsevier LTD., Academic Press. 444 p.

Royle, J.A.; Nichols, J.D. 2003. **Estimating abundance from repeated presence-absence data or point counts.** Ecology. 84(3): 770-790.

Ruhe, R.V. 1975. **Geomorphology: geomorphic processes and surficial geology.** Boston, MA: Houghton Mifflin. 246 p.

Schmid-Holmes, S.; Drickamer, L.C. 2001. **Impact of forest patch characteristics on small mammal communities: a multivariate approach.** Biological Conservation. 99(3): 293-305.

Smolen, M.J. 1981. ***Microtus pinetorum.*** Mammalian Species. 147: 1-7.

Spiegelhalter, D.J.; Thomas, A.; Best, N.; Gilks, W. 1996. **BUGS 0.5: Bayesian inference using Gibbs sampling manual (version ii).** Cambridge, UK: MRC Biostatistics Unit. 59 p.

Spiegelhalter, D.J.; Best, N.G.; Carlin, B.R.; van der Linde, A. 2002. **Bayesian measures of model complexity and fit.** Journal of the Royal Statistical Society Series B--Statistical Methodology. 64(4): 583-616.

Sturtz, S.; Ligges, U.; Gelman, A. 2005. **R2WinBUGS: A package for running WinBUGS from R.** Journal of Statistical Software. 12(3): 1-16.

Urban, N.A. 2010. **Improving inferences on wildlife responses to oak-centered forest management with models that account for imperfect detection.** West Lafayette, IN: Purdue University. 134 p. M.S. thesis.

Urban, N.A.; Swihart, R.K. 2011. **Small mammal responses to forest management for oak regeneration in southern Indiana.** Forest Ecology and Management. 261(3): 353-361.

Wolff, J.O. 1996. **Population fluctuations of mast-eating rodents are correlated with production of acorns.** Journal of Mammalogy. 77(3): 850-856.

Yahner, R.H. 1992. **Dynamics of a small mammal community of a fragmented forest.** The American Midland Naturalist. 127(2): 381-391.

APPENDIX 1.

Sampling data for the probability of detection covariates for the 2 years of trapping at HEE. JD is the first Julian day of trapping for a season at a site. Effort is the number of trapping occasions, Temp is the average daily temperature, and Precip is the presence (= 1) or absence (= 0) of precipitation during and up to 3 hours before trapping.

				Temp (°C) for each day					Precip for each day				
Site	Year	JD	Effort	1	2	3	4	5	1	2	3	4	5
1001	2007	211	264	29	28	27	28	24	0	0	0	0	0
1001	2008	167	282	18	18	20	19	21	1	0	0	0	0
1002	2007	211	287	29	28	24	28	29	0	0	0	0	0
1002	2008	167	273	18	19	18	20	18	1	0	0	0	0
1105	2007	204	274	27	24	23	21	26	0	0	0	0	0
1105	2008	174	283	27	25	26	28	27	0	0	0	0	0
1113	2007	204	295	27	24	25	21	24	0	0	0	1	0
1113	2008	174	283	27	25	26	28	27	0	0	0	0	0
1121	2007	204	296	28	24	23	21	24	0	0	0	1	0
1121	2008	174	246	27	25	26	28	18	0	0	0	0	0
1125	2007	204	292	27	24	24	25	21	0	0	0	0	0
1125	2008	174	291	27	25	26	28	27	0	0	0	0	0
1202	2007	190	292	32	24	24	24	25	0	1	1	0	1
1202	2008	188	277	24	25	26	21	27	0	1	1	0	0
1204	2007	190	277	32	27	25	21	24	0	0	1	0	1
1204	2008	188	283	24	27	24	21	26	0	1	1	0	0
1312	2007	190	254	32	25	26	24	21	0	1	1	0	1
1312	2008	188	280	27	27	25	24	27	1	1	1	0	0
1317	2007	190	252	32	29	26	26	24	0	1	0	0	1
1317	2008	188	214	29	26	27	23	18	1	1	1	0	0
1321	2007	190	279	32	27	26	24	24	0	1	0	0	1
1321	2008	188	258	24	27	26	24	24	1	1	1	0	0
1326	2007	190	242	29	28	26	23	27	0	0	0	0	1
1326	2008	188	233	27	26	24	23	24	1	1	1	0	0
1401	2007	204	290	28	22	22	23	21	0	0	0	0	1
1401	2008	202	283	32	23	24	23	24	1	1	0	0	0
1404	2007	204	286	28	23	23	23	26	0	0	0	0	1
1404	2008	202	283	29	24	21	23	26	0	1	0	0	0
1502	2007	197	292	29	26	27	27	23	0	1	1	1	0
1502	2008	202	280	29	27	25	25	25	0	1	0	0	0
1504	2007	197	281	29	26	24	27	20	0	1	1	1	0
1504	2008	202	287	32	26	25	25	25	1	1	0	0	0

(Appendix 1 continued on next page)

APPENDIX 1 (continued).

Sampling data for the probability of detection covariates for the 2 years of trapping at HEE. JD is the first Julian day of trapping for a season at a site. Effort is the number of trapping occasions, Temp is the average daily temperature, and Precip is the presence (= 1) or absence (= 0) of precipitation during and up to 3 hours before trapping.

				Temp (°C) for each day					Precip for each day				
Site	Year	JD	Effort	1	2	3	4	5	1	2	3	4	5
1602	2007	176	253	31	27	24	26	24	0	0	0	1	1
1602	2008	180	287	21	21	23	24	21	0	0	0	0	1
1622	2007	176	252	24	24	26	26	26	1	0	0	1	0
1622	2008	195	288	27	27	26	27	27	0	0	0	0	0
1624	2007	176	266	27	27	27	25	27	1	0	0	1	0
1624	2008	195	293	27	27	27	27	25	0	0	0	0	0
1627	2007	176	281	27	27	24	27	24	1	0	0	1	0
1627	2008	180	293	21	23	18	21	24	0	0	0	0	1
1703	2007	183	277	29	24	24	26	28	0	0	1	1	0
1703	2008	167	285	18	21	21	20	18	1	0	0	0	0
1705	2007	183	278	27	25	26	25	26	0	0	1	1	0
1705	2008	167	292	18	21	19	19	22	1	0	0	0	0
1716	2007	183	288	27	25	25	28	28	0	0	1	1	0
1716	2008	167	292	18	19	19	19	22	1	0	0	0	0
1728	2007	183	289	29	21	26	24	24	0	0	1	1	0
1728	2008	167	291	18	21	21	20	19	1	0	0	0	0
1803	2007	197	288	29	25	24	26	18	0	1	1	1	0
1803	2008	180	290	21	20	23	18	21	1	0	0	0	1
1820	2007	197	292	29	24	21	18	18	0	1	0	0	0
1820	2008	180	280	21	19	23	24	26	0	0	1	1	1
1821	2007	197	276	29	23	22	27	20	0	0	0	1	0
1821	2008	180	292	21	20	23	24	26	0	0	0	0	1
1830	2007	197	283	29	24	25	24	24	0	1	0	0	0
1830	2008	180	296	21	20	24	19	22	0	0	0	0	1
1907	2007	211	289	29	24	28	28	29	0	0	0	0	0
1907	2008	195	294	29	21	28	27	24	0	0	0	0	0
1908	2007	211	293	29	20	20	21	21	0	0	0	0	0
1908	2008	195	296	29	27	24	28	28	0	0	0	0	0
1917	2007	211	292	28	21	26	27	28	0	0	0	0	0
1917	2008	195	283	29	21	24	27	23	0	0	0	0	0
1919	2007	211	280	27	26	24	27	28	0	0	0	0	0
1919	2008	195	291	29	27	27	26	26	0	0	0	0	0

APPENDIX 2.

Code for the multi-season hierarchical multi-species site occupancy model implemented within a Bayesian framework. This code includes the incorporation of survival and colonization parameters. It was run using software packages R 2.6.1 and WinBUGS using add-on package R2WinBUGS.

```
##data files
##encounter history data from 2007
##7 rows of species encounter histories
##columns of sites
my.2007=read.table(file="HEE_psi_2007.csv", header=T, sep=",",
row.names=1)
##encounter history data from 2008
##7 rows of species encounter histories
##columns of sites
my.2008=read.table(file="HEE_psi_2008.csv", header=T, sep=",",
row.names=1)
##covariate data from 2007
##14 rows of covariate data
##columns of sites
my.cov07=read.table(file="HEE_cov.csv", header=F, sep=",",
row.names=1)
##covariate data from 2008
##14 rows of covariate data
##columns of sites
my.cov08=read.table(file="HEE_cov2.csv", header=F, sep=",",
row.names=1)
##organizing encounter history data into an array
my.data2<-array(data=NA, dim=c(7,32,2))
my.year1<-as.matrix(my.2007)
my.year2<-as.matrix(my.2008)
my.data2[,,1]<-my.year1
my.data2[,,2]<-my.year2
my.data<-array(data=NA, dim=c(7,32,2,1))
my.data[,,,1]<-my.data2
##organizing even-aged treatment covariate into array for
input
my.T1_1<-array(data=NA, dim=c(32,2))
cov.T1_07<-as.matrix(my.cov07[2,])
cov.T1_08<-as.matrix(my.cov08[2,])
my.T1_1[,1]<-cov.T1_07
my.T1_1[,2]<-cov.T1_08
my.T1<-array(data=NA, dim=c(32,2,1))
116
my.T1[,,1]<-my.T1_1
##organizing uneven-aged treatment covariate into array for
input
my.T2_1<-array(data=NA, dim=c(32,2))
cov.T2_07<-as.matrix(my.cov07[3,])
cov.T2_08<-as.matrix(my.cov08[3,])
my.T2_1[,1]<-cov.T2_07
my.T2_1[,2]<-cov.T2_08
```

APPENDIX 2 (continued).

```
my.T2<-array(data=NA, dim=c(32,2,1))
my.T2[,,1]<-my.T2_1
##organizing basal area covariate into array for input
my.ba_1<-array(data=NA, dim=c(32,2))
cov.ba_07<-as.matrix(my.cov07[14,])
cov.ba_08<-as.matrix(my.cov08[14,])
my.ba_1[,1]<-cov.ba_07
my.ba_1[,2]<-cov.ba_08
my.ba<-array(data=NA, dim=c(32,2,1))
my.ba[,,1]<-my.ba_1
##organizing aspect covariate into array for input
my.aspect_1<-array(data=NA, dim=c(32,2))
cov.aspect_07<-as.matrix(my.cov07[5,])
cov.aspect_08<-as.matrix(my.cov08[5,])
my.aspect_1[,1]<-cov.aspect_07
my.aspect_1[,2]<-cov.aspect_08
my.aspect<-array(data=NA, dim=c(32,2,1))
my.aspect[,,1]<-my.aspect_1
##organizing temperature detection covariate into array for
input
my.temp_1<-array(data=NA, dim=c(32,2))
cov.temp_07<-as.matrix(my.cov07[7,])
cov.temp_08<-as.matrix(my.cov08[7,])
my.temp_1[,1]<-cov.temp_07
my.temp_1[,2]<-cov.temp_08
my.temp<-array(data=NA, dim=c(32,2,1))
my.temp[,,1]<-my.temp_1
##organizing Julian day detection covariate into array for input
117
my.jd_1<-array(data=NA, dim=c(32,2))
cov.jd_07<-as.matrix(my.cov07[12,])
cov.jd_08<-as.matrix(my.cov08[12,])
my.jd_1[,1]<-cov.jd_07
my.jd_1[,2]<-cov.jd_08
my.jd<-array(data=NA, dim=c(32,2,1))
my.jd[,,1]<-my.jd_1
#treat occupancy covariates and p covariates the same until
#the logit step
Ymat=my.data #my presence/absence data
mycov=my.cov #my covariates data
nrepls=5 #days sampled, monday through friday
##monitor amount of time it took to run
start.time=Sys.time()
n = dim(my.data)[1] #number of species indicated by number of
rows
nsites = dim(my.data)[2] #number of sites indicated by number
of columns
nyear=dim(my.data)[3]
nfiller=dim(my.data)[4]
#create arguments for bugs()
##input data
```

APPENDIX 2 (continued).

```
data = list(n=n, R=nsites, J=nrepls, Y=my.data, T=nyear, Q=nfiller,
c.T1=my.T1, c.T2=my.T2, c.aspect=my.aspect, c.ba=my.ba,
c.jd=my.jd, c.temp=my.temp)
##parameters listed after model runs
params = list( 'alpha', 'beta', 'beta1','beta2',
##T1surv = survival dependent on even-aged treatment,
T1col=colonization dependent on uneven-aged trtment
'T1','T1surv','T1col',
'T2','T2surv','T2col',
'aspect','aspectsurv','aspectcol',
'ba','basurv','bacol',
'temp',
'jd',
118
'rho', 'sigma.u', 'sigma.v',
'sigma.u1', 'sigma.v1', 'sigma.u2', 'sigma.v2',
's.T1','s.T1surv','s.T1col',
's.T2','s.T2surv','s.T2col',
's.aspect','s.aspectsurv','s.aspectcol',
's.ba','s.basurv','s.bacol',
's.jd',
's.temp',
'phi', 'eta',
'pvec',
'lphi0', 'lgamma0',
'psivec',
'phisurv',
'gamma',
'phiyr','gammayr'
'Z')
## initials
inits = function () {
psi.meanGuess = runif(1, .25, 1)
psi.mean1Guess = runif(1, .25, 1)
psi.mean2Guess = runif(1, .25, 1)
p.meanGuess = runif(1, .25, 1)
## initial values for covariates
beta.T1 = runif(1, 0, 1)
beta.T1col = runif(1, 0, 1)
beta.T1surv = runif(1, 0, 1)
beta.T2col = runif(1, 0, 1)
beta.T2surv = runif(1, 0, 1)
beta.T2 = runif(1, 0, 1)
beta.aspect = runif(1, 0, 1)
beta.aspectcol = runif(1, 0, 1)
beta.aspectsurv = runif(1, 0, 1)
beta.ba = runif(1, 0, 1)
beta.bacol = runif(1, 0, 1)
beta.basurv = runif(1, 0, 1)
beta.temp = runif(1, 0, 1)
beta.jd = runif(1, 0, 1)
```

APPENDIX 2 (continued).

```
rhoGuess = runif (1, 0, 1)
sigma.uGuess = runif (1, 0, 1.5)
sigma.vGuess = runif (1, 0, 1.5)
sigma.u1Guess = runif (1, 0, 1.5)
sigma.v1Guess = runif (1, 0, 1.5)
sigma.u2Guess = runif (1, 0, 1.5)
119
sigma.v2Guess = runif (1, 0, 1.5)
sigma.T1 = runif(1, 0, 1)
sigma.T1surv = runif(1, 0, 1)
sigma.T1col = runif(1, 0, 1)
sigma.T2 = runif(1, 0, 1)
sigma.T2surv = runif(1, 0, 1)
sigma.T2col = runif(1, 0, 1)
sigma.aspect = runif(1, 0, 1)
sigma.aspectsurv = runif(1, 0, 1)
sigma.aspectcol = runif(1, 0, 1)
sigma.ba = runif(1, 0, 1)
sigma.basurv = runif(1, 0, 1)
sigma.bacol = runif(1, 0, 1)
sigma.temp = runif (1, 0, 1)
sigma.jd = runif (1, 0, 1)
list(psi.mean=psi.meanGuess, p.mean=p.meanGuess,
psi.mean1=psi.mean1Guess,
psi.mean2=psi.mean2Guess,
b.T1=beta.T1,
b.T1surv=beta.T1surv,
b.T1col=beta.T1col,
b.T2=beta.T2,
b.T2surv=beta.T2surv,
b.T2col=beta.T2col,
b.aspect=beta.aspect,
b.aspectsurv=beta.aspectsurv,
b.aspectcol=beta.aspectcol,
b.ba=beta.ba,
b.basurv=beta.basurv,
b.bacol=beta.bacol,
b.temp=beta.temp,
b.jd=beta.jd,
sigma.u=sigma.uGuess, sigma.v=sigma.vGuess,
rho=rhoGuess,
sigma.u1=sigma.u1Guess, sigma.v1=sigma.v1Guess,
sigma.u2=sigma.u2Guess, sigma.v2=sigma.v2Guess,
s.T1=sigma.T1,
s.T1surv=sigma.T1surv,
s.T1col=sigma.T1col,
s.T2=sigma.T2,
s.T2surv=sigma.T2surv,
s.T2col=sigma.T2col,
120
s.aspect=sigma.aspect,
```

APPENDIX 2 (continued).

```
s.aspectsurv=sigma.aspectsurv,
s.aspectcol=sigma.aspectcol,
s.ba=sigma.ba,
s.basurv=sigma.basurv,
s.bacol=sigma.bacol,
s.temp=sigma.temp,
s.jd=sigma.jd,
phi=rnorm(n*nfiller, log(psi.meanGuess/(1-psi.meanGuess)),
sigma.uGuess),
lphi0=rnorm(n, log(psi.mean1Guess/(1-psi.mean1Guess)),
sigma.u1Guess),
lgamma0=rnorm(n, log(psi.mean2Guess/(1-psi.mean2Guess)),
sigma.u2Guess),
eta=rnorm(n*nfiller, log(p.meanGuess/(1-p.meanGuess)), sigma.vGuess),
T1=rnorm(n*nfiller, log(beta.T1/(1-beta.T1)), sigma.T1),
T1surv=rnorm(n*nfiller, log(beta.T1surv/(1-beta.T1surv)), sigma.T1surv),
T1col=rnorm(n*nfiller, log(beta.T1col/(1-beta.T1col)), sigma.T1col),
T2=rnorm(n*nfiller, log(beta.T2/(1-beta.T2)), sigma.T2),
T2surv=rnorm(n*nfiller, log(beta.T2surv/(1-beta.T2surv)), sigma.T2surv),
T2col=rnorm(n*nfiller, log(beta.T2col/(1-beta.T2col)), sigma.T2col),
aspect=rnorm(n*nfiller, log(beta.aspect/(1-beta.aspect)), sigma.aspect),
aspectsurv=rnorm(n*nfiller, log(beta.aspectsurv/(1-beta.aspectsurv)),
sigma.aspectsurv),
aspectcol=rnorm(n*nfiller, log(beta.aspectcol/(1-beta.aspectcol)),
sigma.aspectcol),
ba=rnorm(n*nfiller, log(beta.ba/(1-beta.ba)), sigma.ba),
basurv=rnorm(n*nfiller, log(beta.basurv/(1-beta.basurv)), sigma.basurv),
bacol=rnorm(n*nfiller, log(beta.bacol/(1-beta.bacol)), sigma.bacol),
temp=rnorm(n*nfiller, log(beta.temp/(1-beta.temp)), sigma.temp),
jd=rnorm(n*nfiller, log(beta.jd/(1-beta.jd)), sigma.jd),
Z = array(rbinom(n*nsites, size=1, prob=psi.meanGuess),
dim=c(7,32,2,1))
)}
modelFilename <- "MSOMKN.txt"
###defining model and priors
cat("
model {
121
psi.mean ~ dunif (0,1)
psi.mean1 ~ dunif (0,1)
psi.mean2 ~ dunif (0,1)
beta <- log(psi.mean) - log(1-psi.mean)
beta1 <- log(psi.mean1) - log(1-psi.mean1)
beta2 <- log(psi.mean2) - log(1-psi.mean2)
b.T1 ~ dunif(0,1)
b.T1surv ~ dunif(0,1)
b.T1col ~ dunif(0,1)
b.T2 ~ dunif(0,1)
b.T2surv ~ dunif(0,1)
b.T2col ~ dunif(0,1)
b.aspect ~ dunif(0,1)
```

APPENDIX 2 (continued).

```
b.aspectsurv ~ dunif(0,1)
b.aspectcol ~ dunif(0,1)
b.ba ~ dunif(0,1)
b.basurv ~ dunif(0,1)
b.bacol ~ dunif(0,1)
b.temp ~ dunif(0,1)
b.jd ~ dunif(0,1)
mu.T1<-log(b.T1/(1-b.T1))
mu.T1surv<-log(b.T1surv/(1-b.T1surv))
mu.T1col<-log(b.T1col/(1-b.T1col))
mu.T2<-log(b.T2/(1-b.T2))
mu.T2surv<-log(b.T2surv/(1-b.T2surv))
mu.T2col<-log(b.T2col/(1-b.T2col))
mu.aspect<-log(b.aspect/(1-b.aspect))
mu.aspectsurv<-log(b.aspectsurv/(1-b.aspectsurv))
mu.aspectcol<-log(b.aspectcol/(1-b.aspectcol))
mu.ba<-log(b.ba/(1-b.ba))
mu.basurv<-log(b.basurv/(1-b.basurv))
mu.bacol<-log(b.bacol/(1-b.bacol))
mu.temp<-log(b.temp/(1-b.temp))
122
mu.jd<-log(b.jd/(1-b.jd))
sigma.u ~ dunif (0,10)
sigma.v ~ dunif (0,10)
sigma.u1 ~ dunif (0,10)
sigma.v1 ~ dunif (0,10)
sigma.u2 ~ dunif (0,10)
sigma.v2 ~ dunif (0,10)
s.T1 ~ dunif(0,10)
s.T1surv ~ dunif(0,10)
s.T1col ~ dunif(0,10)
s.T2 ~ dunif(0,10)
s.T2surv ~ dunif(0,10)
s.T2col ~ dunif(0,10)
s.aspect ~ dunif(0,10)
s.aspectsurv ~ dunif(0,10)
s.aspectcol ~ dunif(0,10)
s.ba ~ dunif(0,10)
s.basurv ~ dunif(0,10)
s.bacol ~ dunif(0,10)
s.temp ~ dunif(0,10)
s.jd ~ dunif(0,10)
tau.u <- pow(sigma.u,-2)
tau.v <- pow(sigma.v,-2)
tau.u1 <- pow(sigma.u1,-2)
tau.v1 <- pow(sigma.v1,-2)
tau.u2 <- pow(sigma.u2,-2)
tau.v2 <- pow(sigma.v2,-2)
tau.T1<-pow(s.T1, -2)
tau.T1surv<-pow(s.T1surv, -2)
tau.T1col<-pow(s.T1col, -2)
```

APPENDIX 2 (continued).

```
tau.T2<-pow(s.T2, -2)
123
tau.T2surv<-pow(s.T2surv, -2)
tau.T2col<-pow(s.T2col, -2)
tau.aspect<-pow(s.aspect, -2)
tau.aspectsurv<-pow(s.aspectsurv, -2)
tau.aspectcol<-pow(s.aspectcol, -2)
tau.ba<-pow(s.ba, -2)
tau.basurv<-pow(s.basurv, -2)
tau.bacol<-pow(s.bacol, -2)
tau.temp<-pow(s.temp, -2)
tau.jd<-pow(s.jd, -2)
rho ~ dunif(-1,1)
var.eta <- tau.v/(1.-pow(rho,2))
for(i in 1:n) {
phi[i] ~ dnorm(beta, tau.u)I(-5,5)
T1[i] ~ dnorm(mu.T1, tau.T1)I(-5,5)
T1surv [i] ~ dnorm(mu.T1surv, tau.T1surv)I(-5,5)
T1col [i] ~ dnorm(mu.T1col, tau.T1col)I(-5,5)
T2[i] ~ dnorm(mu.T2, tau.T2)I(-5,5)
lphi0 [i] ~ dnorm(beta1, tau.u1)I(-5,5)
T2surv [i] ~ dnorm(mu.T2surv, tau.T2surv)I(-5,5)
##T2 covariate for survival parameter
lgamma0 [i] ~ dnorm(beta2, tau.u2)I(-5,5)
##lgamma0 coefficient for intercept
T2col [i] ~ dnorm(mu.T2col, tau.T2col)I(-5,5)
##T2 covariate for colinization parameter
aspect[i] ~ dnorm(mu.aspect, tau.aspect)I(-5,5)
aspectsurv [i] ~ dnorm(mu.aspectsurv, tau.aspectsurv)I(-5,5)
aspectcol [i] ~ dnorm(mu.aspectcol, tau.aspectcol)I(-5,5)
ba[i] ~ dnorm(mu.ba, tau.ba)I(-5,5)
basurv [i] ~ dnorm(mu.basurv, tau.basurv)I(-5,5)
bacol [i] ~ dnorm(mu.bacol, tau.bacol)I(-5,5)
temp[i] ~ dnorm(mu.temp, tau.temp)I(-5,5)
jd[i] ~ dnorm(mu.jd, tau.jd)I(-5,5)
}
p.mean ~ dunif (0,1)
124
alpha <- log(p.mean) - log(1-p.mean)
for(i in 1:n){
mu.eta[i] <- alpha + (rho*sigma.v/sigma.u)*(phi[i] - beta)
eta[i] ~ dnorm(mu.eta[i], var.eta)I(-5,5)
}
# at logit(psi) you should add your occupancy covariates and
for logit(p) you should
#add your detection covariates
for (i in 1:n){
for (k in 1:R) {
for (t in 1:T){
for (z in 1:Q){
logit(p[i,k,t,z]) <-eta[i]+jd[i]*c.jd[k,t,z]+temp[i]*c.temp[k,t,z]
```

APPENDIX 2 (continued).

```
}}}}
#State Submodel
# initial state and likelihood for year = 1
#first year occupancy
for (i in 1:n){
for (k in 1:R) {
for (t in 1:1){
for (z in 1:Q){
logit(psi[i,k,t,z]) <-phi[i]
+T1[i]*c.T1[k,1,z]
+T2[i]*c.T2[k,1,z]
+aspect[i]*c.aspect[k,1,z]
+ba[i]*c.ba[k,1,z]
Z[i,k,1,z] ~ dbern(psi[i,k,1,z])
mu.p[i,k,1,z] <- p[i,k,1,z]*Z[i,k,1,z]
Y[i,k,1,z] ~ dbin(mu.p[i,k,1,z], J)
}}}}
##determining survival and colonization
##for year 1 to 2
for (i in 1:n){
for (k in 1:R) {
for (t in 2:2){
for (z in 1:Q){
logit(phisurv[i,k,t-1,z]) <- lphi0[i]
+T1surv[i]*c.T1[k,1,z]
+T2surv[i]*c.T2[k,1,z]
+aspectsurv[i]*c.aspect[k,1,z]
125
+basurv[i]*c.ba[k,1,z]
logit(gamma[i,k,t-1,z]) <- lgamma0[i]
+T1col[i]*c.T1[k,1,z]
+T2col[i]*c.T2[k,1,z]
+aspectcol[i]*c.aspect[k,1,z]
+bacol[i]*c.ba[k,1,z]
mu[i,k,t,z]<-Z[i,k,t-1,z]*phisurv[i,k,t-1,z]
+ (1-Z[i,k,t-1,z])*gamma[i,k,t-1,z]
Z[i,k,t,z] ~ dbern(mu[i,k,t,z])
mu.p[i,k,t,z] <- p[i,k,t,z]*Z[i,k,t,z]
Y[i,k,t,z] ~ dbin(mu.p[i,k,t,z], J)
}}}}
# Derived parameters: Compute annual occupancy and growth
rates
for (i in 1:n){
psivec[i,1]<-mean(psi[i,1:R,1,1])
pvec[i,1]<-mean(p[i,1:R,1:T,1])
phiyr[i,1]<-mean(phisurv[i,1:R,1,1])
gammayr[i,1]<-mean(gamma[i,1:R,1,1])
}
for(i in 1:n){
for(j in 2:2){
psivec[i,j] <- psivec[i,j-1]*phiyr[i,j-1]
```

APPENDIX 2 (continued).

```
+ (1-psivec[i,j-1])*gammayr[i,j-1]
growthr[i,j]<- psivec[i,j]/psivec[i,j-1]
turnover[i,j-1]<- ((1 - psivec[i,j-1]) * gammayr[i,j-1])/( (1 -
psivec[i,j-1]) * gammayr[i,j-1]
+ phiyr[i,j-1]*psivec[i,j-1])
eop[i,j-1]<- (gammayr[i,j-1])/( (gammayr[i,j-1])
+ (1-phiyr[i,j-1]))
}}}
", fill=TRUE, file=modelFilename)
#fit model to data using WinBUGS code, make sure to have
WinBUGS installed
#with the appropriate key decoded
library(R2WinBUGS)
fit = bugs(data, inits, parameters.to.save=params,
model.file=modelFilename,
n.chains=5, n.iter=55000, n.burnin=5000, n.thin=50,
bugs.seed=sample(1:9999,size=1), debug=T, DIC=F, coda=T)
126
end.time=Sys.time()
elapsed.time= difftime(end.time, start.time, units='mins')
cat(paste(paste('Posterior computed in ', elapsed.time, sep=''), '
minutes\n', sep=''))
```