

1 ***Peromyscus* responses to alternative forest management systems in the**  
2 **Missouri Ozarks, USA**

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## 21 Abstract

22 Operational-scale forest management experiments are long-term investments because harvest  
23 treatment effects may be dynamic throughout one or more rotation lengths. We examined  
24 deer mouse (*Peromyscus* spp.) abundance over the first 20 years of the Missouri Ozark Forest  
25 Ecosystem Project (MOFEP), which assesses ecological responses to even-aged, uneven-aged,  
26 and no-harvest forest management systems applied at landscape scales in the Missouri Ozarks. In  
27 the spring of each of 11 sampling years, we sampled *Peromyscus* populations on two permanent  
28 trap grids on each of the nine study sites ( $n = 3$  sites per management system). Management  
29 entries occurred in 1996 and 2011, with small mammal sampling conducted during two pre-  
30 treatment years (1994–1995), and Years 2–5 (1998–2001), Years 13–14 (2009–2010), and Years  
31 16–18 (2012–2014) after the first entry. We estimated abundance for each grid in each sampling  
32 year with Bayesian closed-population mark-recapture models, and modeled variation in  
33 abundance with negative binomial log-linear mixed effects models. Uneven- and even-aged  
34 management systems caused similar increases in *Peromyscus* abundance that were detectable  
35 shortly after the first management entry [proportional effect of even-aged management on  
36 *Peromyscus* abundance vs. no-harvest management: posterior median = 1.8, 95% credible  
37 interval 1.0–3.2; proportional effect of uneven-aged vs. no harvest management = 1.7 (1.0, 2.8)].  
38 These effects were not surprising given positive effects of harvest treatments on understory cover  
39 and food resources. However, the consistency of this increase was less expected, as we observed  
40 no conclusive dissipation of harvest effects even in Years 13–14 after the first entry or  
41 amplification of harvest effects after the second entry. Observing extremely high system-wide  
42 yearly variation in *Peromyscus* abundance, we did not detect evidence of increasing divergence  
43 in effects of these three management systems or of any area-wide trends in abundance during

44 1994–2014. However, over subsequent decades, we expect higher potential for divergence in  
45 *Peromyscus* abundance as the three management systems differentially shape forest structure and  
46 tree species composition. Thus, the MOFEP study offers a unique framework for building and  
47 testing hypotheses about patterns and mechanisms of long-term changes in Ozark forests and  
48 effects on vertebrate communities.

49

## 50 **Keywords**

51 Deermice; Even-aged management; Missouri Ozarks; MOFEP; Small mammals; Uneven-aged  
52 management

53

54

## 55 **1. Introduction**

56 Controlled experiments at operational scales allow direct statistical inference about effects of  
57 forest management treatments, using randomization and pre-treatment measures to reduce effects  
58 of potential confounding factors that may be impossible to address adequately in non-  
59 experimental studies (Ganio, 2006; Monserud, 2002; Sheriff and He, 1997). However, when  
60 experimental treatments involve harvesting mature forests, such studies face the challenge that  
61 the full responses to forest disturbances can unfold over temporal scales ranging from short-term  
62 immediate effects and year-to-year early successional dynamics, to decadal- and century-scale  
63 changes (Franklin et al., 2002; Gill et al., 2017; Lindenmayer and Laurance, 2012; Oliver, 1980;  
64 Olson and Saunders, 2017). This challenge is especially relevant for understanding responses by  
65 forest-floor small mammals, which are a frequent research component of multidisciplinary  
66 operational experiments (Converse et al., 2006; Fantz and Renken, 2005; Kellner et al., 2013;  
67 Lehmkuhl et al., 1999). Although small mammal populations can show especially strong changes

68 in the first few years after canopy-removing disturbances (Gashwiler, 1970b; Kirkland, 1990;  
69 Sullivan et al., 2008), responses are dynamic over subsequent stages of stand development (Ecke  
70 et al., 2002; Fisher and Wilkinson, 2005; Sullivan et al., 1999; Zwolak, 2009). Decades after a  
71 disturbance, small mammal populations may continue to be shaped by the disturbance's long-  
72 term effects on key habitat characteristics such as abundance of large down logs (Carey and  
73 Johnson, 1995) and abundance and species composition of mast-producing trees (Ostfeld et al.,  
74 1996; Wang et al., 2009). Even in the absence of physical disturbances, populations of small  
75 mammal taxa such as deermice (*Peromyscus* spp.) can show enormous temporal variation in  
76 abundance due to extrinsic variability in food resources and weather along with intrinsic effects  
77 of density dependence at intra- to interannual time scales (e.g. Lewellen and Vessey, 1998; Luis  
78 et al., 2010; Wang et al., 2009). Such variation creates the potential for corresponding temporally  
79 heterogeneous population responses to manipulative treatments (sensu, for example, Seamon and  
80 Adler, 1996; Wheatley et al., 2002). Conversely, examining treatment effects in the context of  
81 background spatial and temporal variation may provide a better understanding of the relative  
82 importance of forest management as an agent of population change.

83         One of the longest-active multidisciplinary forestry experiments using large-scale  
84 operational treatments is the Missouri Ozark Forest Ecosystem Project (MOFEP) in southeastern  
85 Missouri, USA (Knapp et al., 2014). This Missouri Department of Conservation (MDC) study  
86 was initiated in the early 1990s to help managers better understand the impacts of harvest  
87 practices in state-owned forests of the region. Intended to be a multi-century study, MOFEP  
88 compares long-term application of three operational management systems (i.e. three  
89 experimental treatments: no-harvest management, uneven-aged management, and even-aged  
90 management) applied on a 100-year rotation length to several-hundred ha experimental sites

91 (Brookshire and Shifley, 1997; Shifley and Kabrick, 2002). Individual management entries occur  
92 periodically, with each entry affecting a subset of the stands within each site. Compared to stand-  
93 level studies, a long-term perspective is especially critical in MOFEP given that experimental  
94 treatments are long-term applications of management systems at the scale of local landscapes.  
95 After two decades of data collection in core research areas (Knapp et al., 2014), the experiment  
96 has reached a uniquely valuable stage in which researchers and managers can begin comparing  
97 long-term effects of the three management systems (e.g. Morris et al., 2013; Olson et al., 2015;  
98 Olson et al., 2017; Rota et al., 2017).

99         During the first five years post-treatment in MOFEP, uneven- and even-aged  
100 management had similar positive effects on relative abundance of *Peromyscus* spp., the primary  
101 taxa captured in the study's small mammal component (Fantz and Renken, 2005). Specifically,  
102 harvest treatments appeared to buffer populations from an apparent regional multi-year decline in  
103 abundance documented on no-harvest sites. It was unknown whether this multi-year decline was  
104 part of a longer term trend, but this possibility highlights an additional temporal complexity that  
105 can be assessed with long-term studies. Operational experiments such as MOFEP take place in  
106 forest ecosystems that may be undergoing broader directional changes due to factors such as  
107 climate change, introduced diseases, and altered disturbance patterns (Gillen and Hellgren, 2013;  
108 Hanberry et al., 2014; Olson et al., 2014; Zenner et al., 2006). Thus, there is potential for  
109 interactions between experimental treatments and larger scale agents of change (Olson et al.,  
110 2017).

111         Building on previous work by Fantz and Renken (2005), we examined patterns of change  
112 in *Peromyscus* abundance for 11 years of sampling during the first 20 years of the MOFEP small  
113 mammal study. Timing of sampling was tied to the first (1996) and second (2011) management

114 entries. Sampling occurred in four groups of years: pre-treatment (1994–1995), and Years 2–5  
115 (1998–2001), Years 13–14 (2009–2010), and Years 16–18 (2012–2014) after the first  
116 management entry, with the last group covering the first three years after the second  
117 management entry. We focused on several questions about comparative effects of MOFEP  
118 treatments on *Peromyscus* abundance. First, we examined whether the positive initial effects of  
119 uneven- and even-aged harvest treatments noted by Fantz and Renken (2005) persisted over a  
120 decade (13–14 years) after the first management entry. Second, we assessed whether short-term  
121 population changes after the second management entry showed similar patterns as those  
122 observed after the first entry. Third, to give context for the relative importance of harvest  
123 treatments as drivers of *Peromyscus* population abundance, we compared treatment effects to the  
124 range of background variation among years and sites in this study system. Finally, we assessed  
125 whether there were detectable system-wide trends in *Peromyscus* abundance during the first 20  
126 years of the MOFEP study, particularly treatment-specific trends that would indicate divergence  
127 among management approaches.

128

## 129 **2. Materials and methods**

### 130 **2.1. MOFEP design**

131 We provide a brief description of MOFEP's experimental design, study sites, and small mammal  
132 sampling protocol; other publications provide more extensive details (Brookshire and Shifley,  
133 1997; Knapp et al., 2014; Shifley and Kabrick, 2002). The study occurs in the south-central  
134 Missouri Ozark Highlands, in mature, second-growth forests dominated by oaks (*Quercus* spp.),  
135 hickories (*Carya* spp.), other hardwoods, and shortleaf pine (*Pinus echinata*). Any prior timber  
136 harvesting on study sites occurred before 1950. The experiment uses a complete randomized

137 block design, with three blocks each consisting of three, 312–514-ha sites (Sheriff and He,  
138 1997). Each of three experimental treatments [no harvest (NH), uneven-aged (UA), or even-aged  
139 (EA) management systems] was randomly assigned to one site per block. Uneven-aged and  
140 even-aged management systems follow MDC management guidelines current at the time of each  
141 entry (e.g. MDC, 2014), with management entries planned every 15 years such that sites are  
142 managed on a 100-year rotation for uneven- and even-aged systems.

143         Each study site comprises a local landscape of 44–82 individual forest stands.  
144 Manipulations applied at the stand level are components of each management system (e.g.  
145 clearcut harvests in even-aged management), but are not applied to all stands within a site at each  
146 entry. Rather, decisions about whether and how to treat each stand during each entry are based  
147 on stand and site characteristics as in standard operational management, albeit within the bounds  
148 of the randomly assigned site-level management approach (Sheriff, 2002). Thus, the primary  
149 focus of MOFEP is the comparative landscape-scale effects of long-term application of these  
150 management systems rather than stand-level effects of individual entries.

151         To date, treatment entries have occurred in 1996 and 2011. In even-aged treatments,  
152 during each of the two entries 10–15% of each site was regeneration harvested (clearcut) in  
153 openings 3–12 ha in size, with up to 2.3 m<sup>2</sup> ha<sup>-1</sup> residual basal area retained in clearcut areas  
154 (Knapp et al., 2014). In 2011, 11% of one even-aged treatment site was shelterwood harvested.  
155 In both entries, other stands on even-aged sites received intermediate thinning (average of 15.7%  
156 of site area per entry, Knapp et al., 2014) or were not treated. In sites assigned to uneven-aged  
157 management, during the first entry, single-tree and small group selection harvests occurred on  
158 much of each site (average area harvested = 57%, Kabrick et al., 2002). Group selection harvests  
159 were implemented on approximately 5% of the non-reserved area of each uneven-aged site

160 during the 1996 entry, producing 123–267 small (21–43 m diameter) openings throughout these  
161 sites. In the second management entry, only single-tree selection was implemented on uneven-  
162 aged sites (averaging 40% of each site; Knapp et al., 2014). Variation in the specific actions  
163 implemented as part of each management system (e.g. group-selection harvests with uneven-  
164 aged management) reflect that experimental treatments are the long-term, site-level application  
165 of operational systems, which allow management flexibility within and between entries (Knapp  
166 et al., 2014). The average site-level residual basal area after each entry was similar between  
167 uneven- and even-aged treatments (approx.  $17\text{--}19\text{ m}^2\text{ ha}^{-1}$  immediately after each entry vs.  
168 average approx.  $23\text{--}24\text{ m}^2\text{ ha}^{-1}$  in no-harvest treatment sites; Olson et al., 2017). During each  
169 entry approximately 10% of each uneven- and even-aged site was reserved and not subject to  
170 harvest in that entry.

171

## 172 **2.2. Small mammal sampling**

173 The MOFEP small mammal design restricted inference to north- and east-facing side slopes  
174 within each site (Fantz and Renken, 2005). Within this land type, two  $12 \times 12$  permanent  
175 trapping grids were established per site, with 25 m between trap stations, resulting in 18 grids of  
176 7.6 ha each. Because of MOFEP's long-term focus on management systems applied at the site  
177 level, these permanent grids were established in each site without respect to where stand-level  
178 manipulations occur during individual management entries. Trap stations of grids in uneven-aged  
179 treatment sites were mostly in areas harvested during the first entry ( $\bar{x} = 92\%$  of stations per grid,  
180 range 75–100%, including 6–11% of stations per grid exposed to group-selection harvests), but  
181 exposure was lower and more variable in the second harvest entry ( $\bar{x} = 30\%$  of stations, range 0–  
182 83%). In even-aged treatment sites, 0–98% of stations per grid entry were exposed to



183 regeneration harvests or intermediate thinning (first entry:  $\bar{x}$  = 28%, range = 0–60% of stations  
184 per grid; second entry:  $\bar{x}$  = 56%, range = 0–98%). All grids were separated by at least 300 m;  
185 throughout all sampling we recorded between-grid movements by <5 mice.

186         During spring (April and May) of each sampling year, each grid was sampled for a single  
187 trap session during which traps were open continuously for six consecutive days and nights, and  
188 checked daily. Sites within a block were trapped simultaneously, while the three blocks were  
189 trapped non-simultaneously during each sampling year. A single Sherman live trap ( $7.7 \times 8.9 \times$   
190  $22.9$  cm) (H.B. Sherman Trap, Inc., Tallahassee, Fla., USA) was placed at each station, baited  
191 with a mixture of peanut butter and oats, and rebaited as needed during each daily trap check. At  
192 each trap check, captured live animals were identified to species, marked, and released.

193 *Peromyscus* were uniquely marked with toe clipping (1994–2010) or numbered ear tags (2012–  
194 2014); other taxa were marked with these methods or marked temporarily with a non-toxic  
195 permanent black marker.

196

### 197 **2.3. Analytical methods**

198 Analyses focused on combined abundance of *Peromyscus maniculatus* (North American  
199 deermouse) and *P. leucopus* (white-footed deermouse), as other taxa were captured infrequently.

200 As discussed by Fantz and Renken (2005), morphological field discrimination of these two

201 *Peromyscus* species was problematic. Moreover, both species appeared to be common

202 throughout our sampling; in this system, patterns of combined abundance were considered to be

203 of higher management relevance than their species-specific responses (R. Renken, pers. obs.).

204 Naïve apparent survival between years was close to 0 for *Peromyscus*, so we treated each yearly

205 six-night trap session as a closed-population mark-recapture sample, resulting in 198 sessions

206 (i.e. 9 sites  $\times$  2 grids per site  $\times$  11 sampling years). To quantify changes in abundance, we first  
207 attempted a fully integrated Bayesian hierarchical modeling approach following Schofield and  
208 Barker (2014) and Converse and Royle (2012), but experienced prohibitively slow convergence  
209 and long processing time during extensive preliminary modeling of the large MOFEP data set  
210 with these approaches (see Appendix). Therefore, we performed a two-stage analysis, first  
211 estimating abundance via mark-recapture modeling, then using these abundance estimates as the  
212 response variable for modeling variation in expected abundance.

213

### 214 **2.3.1. Mark-recapture estimation**

215 We implemented Bayesian closed-population mark-recapture modeling to estimate abundance  
216 for each of the 198 sessions in a unified analysis (Kéry and Schaub, 2012; Royle and Dorazio,  
217 2008; Royle et al., 2007). Full details are available in the Appendix. The primary detectability  
218 model we used was a form of the general model  $M_{tb}$  (Otis et al., 1978) incorporating within-  
219 session variability in capture probabilities due to temporal effects and behavioral response to  
220 prior capture. Posterior distributions were estimated via Markov Chain Monte Carlo (MCMC)  
221 sampling using JAGS 4.2.0 and R library rjags (Plummer, 2016). We report posterior  
222 distributions for session-specific abundance, across-session average per-night capture  
223 probability, and the across-session average recapture effect. The recapture effect was reported on  
224 the odds ratio scale (odds of recapture if captured on the previous trap night / odds of capture if  
225 not captured on the previous trap night), with the posterior distribution estimated by  
226 exponentiating the logit-scale average recapture effect parameter within each MCMC iteration.  
227 For all analyses, posterior distributions for each parameter were summarized by the posterior  
228 median and a 95% credible interval formed by taking the (0.025, 0.975) percentiles of the

229 posterior samples. Our second stage of analyses used these mark-recapture abundance posterior  
230 distributions to form response variables for analyzing patterns of abundance across sites and  
231 years.

232

### 233 **2.3.2. Abundance modeling**

234 For modeling expected abundance, we used alternative forms of a general negative binomial  
235 mixed effects model, tailoring the parameterization of each form to better address specific  
236 research questions. Our primary second-stage analysis estimated overall and yearly effects of the  
237 three MOFEP experimental treatments, using estimated abundance for each grid for the nine  
238 post-treatment years as the response variable and average pre-treatment estimated abundances  
239 for each grid as a covariate (sensu Senn, 2006). The model included fixed effects of average pre-  
240 treatment abundance and block, and random effects of site, year, and block  $\times$  year (see  
241 Appendix). Log-scale treatment effects were modeled with fixed-effects parameters for the  
242 overall effects of uneven-aged and even-aged management relative to no-harvest management;  
243 these could be interpreted as estimates of average effects of uneven-aged and even-aged  
244 management across all nine post-treatment sampling years. We added a treatment  $\times$  year random  
245 effect allowing for yearly variation in effects of the harvest management systems. We  
246 exponentiated posterior samples of log-scale treatment-contrast parameters to form posterior  
247 distributions for overall and year-specific proportional effects of uneven-aged and even-aged  
248 management on expected *Peromyscus* abundance. We compared harvest treatments by  
249 calculating posterior distributions for the ratio of even-aged to uneven-aged average and year-  
250 specific proportional effects.

251 To examine the implications of ignoring mark-recapture abundance estimation  
252 uncertainty, we conducted two alternative sets of analyses with this treatment-effects model. In  
253 the first analysis ( $N_{posterior\_median}$  analysis), we did not incorporate mark-recapture estimation  
254 uncertainty, but fit the model to the single vector of posterior median abundance estimates from  
255 Bayesian mark-recapture estimation. The pre-treatment abundance covariate was calculated as  
256 the average of the two pre-treatment posterior median estimates for each grid (i.e. average of  
257 1994 and 1995 values). To assess whether posterior uncertainty about model parameters  
258 increased meaningfully when mark-recapture estimation uncertainty was incorporated, we  
259 performed a second analysis ( $N_{posterior\_sample}$  analysis) using individual MCMC sample vectors  
260 from the posterior distributions for session-specific abundance from mark-recapture modeling,  
261 rather than just the single posterior median vector. The Bayesian mark-capture modeling of  
262 capture histories from the 198 trap sessions produced 30,000 posterior abundance vectors, each  
263 of length 198. We used each of 3,000 of these posterior sample vectors (every 10<sup>th</sup> multivariate  
264 sample) as input data for the negative binomial treatment-effects model described above, with  
265 the pre-treatment average abundance for each grid calculated using the relevant pre-treatment  
266 abundance values from that sample vector. We analyzed each vector separately to produce 3,000  
267 sets of posterior samples of negative binomial model parameters, then pooled these sets to form  
268 hyper-posterior distributions that incorporated mark-recapture estimation uncertainty. For all  
269 negative binomial abundance models, posterior distributions were estimated with MCMC in Stan  
270 via R packages brms (Buerkner, 2017) and RStan (Stan Development Team, 2016). More  
271 complete details about each analysis are in the Appendix.

272 To better estimate background spatial and temporal effects in the MOFEP system, we ran  
273 a modified form of the negative binomial model with mark-recapture posterior median

274 abundance as the response variable. In this model form, we incorporated pre-treatment  
275 abundance into the response variable vector rather than as a covariate, thus allowing estimation  
276 of 11 rather than 9 year effects and fully incorporating estimates of persistent spatial variation  
277 (other than among-treatment variation) into block and site effects. We calculated posterior  
278 summaries for block-, site- and year-specific effects (see Appendix), and compared their  
279 magnitudes with those of estimated treatment effects from the  $N_{posterior\_median}$  analysis.

280 To assess evidence of long-term trends in *Peromyscus* abundance and whether treatments  
281 showed an increasingly diverging pattern, we focused on a third form of the general negative  
282 binomial mixed effects model using posterior median abundance estimates for years 1994  
283 through 2014 as the response variable. The model incorporated year as a numeric covariate, a  
284 treatment-specific log-linear trend parameter, block fixed effects, and random effects as  
285 described above (see Appendix). Samples for log-scale trend parameters were exponentiated to  
286 produce posterior distributions for proportional trends.

287

### 288 3. Results

289 During 11 sampling years with a combined trap effort of 171,072 trap nights across 198 trap  
290 sessions, we recorded 7,135 captures of at least 4,377 unique individuals. We captured 16  
291 species (Table 1), with *Peromyscus* comprising 88% of individuals captured (3,871 mice).  
292 Individual mice were rarely captured in more than one year, with only 48 *Peromyscus*  
293 individuals recaptured between years for the entire study. Throughout all sampling, 50% of  
294 *Peromyscus* were identified in the field as *P. leucopus* and 43% as *P. maniculatus*; 7% were not  
295 identified to species. Based on morphological identifications, both species were commonly  
296 captured throughout the study; for example, mice identified as *P. maniculatus* comprised 50% of

297 the 757 *Peromyscus* captured in 1994–1995, and 43% of the 1,754 *Peromyscus* captured in  
298 2012–2014.

299 Table 1. Total individual animals captured by taxon during small mammal live trapping on nine  
 300 MOFEP study sites in Missouri Ozarks, USA, 1994–2014. Nomenclature follows Bradley et al,  
 301 2014. (Note: morphological discrimination of *P. maniculatus* from *P. leucopus* was of uncertain  
 302 accuracy; please see Section 2.3.)

| Species                                                        | Individuals |
|----------------------------------------------------------------|-------------|
| Elliot's short-tailed shrew ( <i>Blarina hylophaga</i> )       | 51          |
| Least shrew ( <i>Cryptotis parva</i> )                         | 1           |
| Eastern cottontail ( <i>Sylvilagus floridanus</i> )            | 1           |
| Eastern gray squirrel ( <i>Sciurus carolinensis</i> )          | 2           |
| Southern flying squirrel ( <i>Glaucomys volans</i> )           | 14          |
| Eastern chipmunk ( <i>Tamias striatus</i> )                    | 208         |
| Eastern woodrat ( <i>Neotoma floridana</i> )                   | 160         |
| Fulvous harvest mouse ( <i>Reithrodontomys fulvescens</i> )    | 4           |
| Western harvest mouse ( <i>Reithrodontomys megalotis</i> )     | 11          |
| White-footed deermouse ( <i>Peromyscus leucopus</i> )          | 1912        |
| North American deermouse ( <i>Peromyscus maniculatus</i> )     | 1675        |
| Deermouse, not identified to species ( <i>Peromyscus</i> spp.) | 284         |
| Golden mouse ( <i>Ochrotomys nuttalli</i> )                    | 42          |
| Prairie vole ( <i>Microtus ochrogaster</i> )                   | 1           |
| Woodland vole ( <i>Microtus pinetorum</i> )                    | 9           |
| Southern bog lemming ( <i>Synaptomys cooperi</i> )             | 1           |
| House mouse ( <i>Mus musculus</i> )                            | 1           |

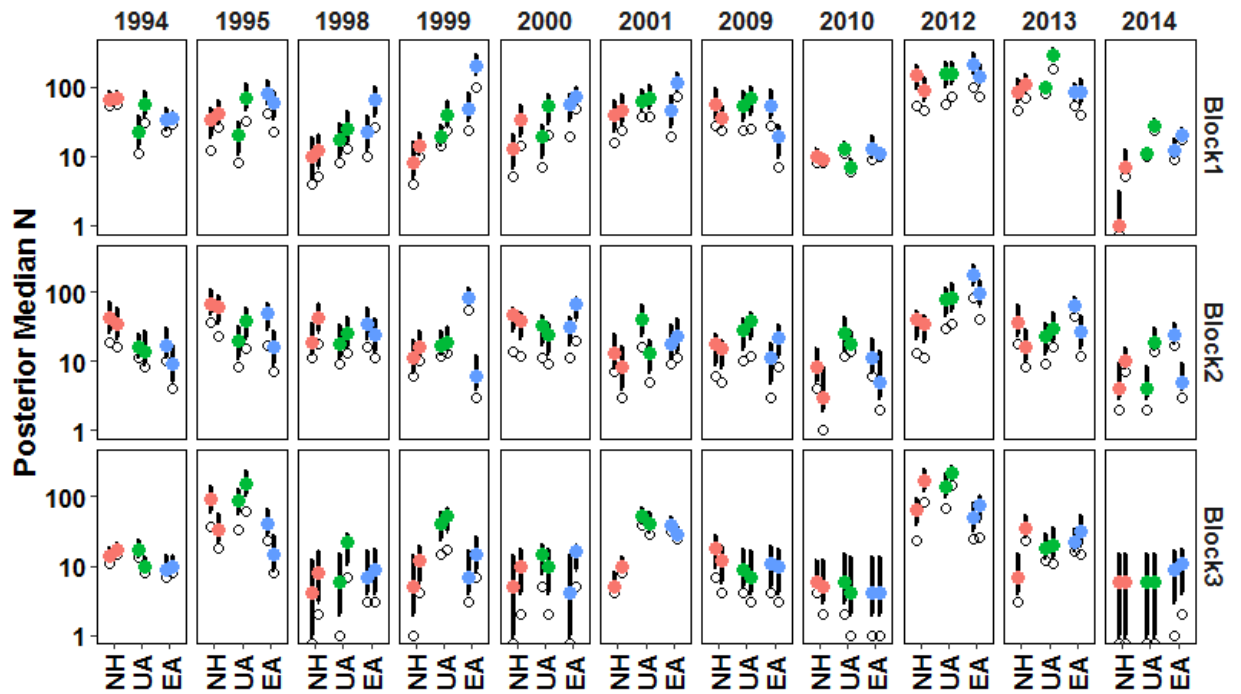
304  
305 Captures per six-night trap session ranged from 0–184 individual *Peromyscus* per grid ( $\bar{x}$   
306 = 19.6, median = 11, SD = 24.4; Fig. 1). Average overall probability of capture for an individual  
307 not previously captured in a trap session was low [posterior median = 0.109, 95% credible  
308 interval = 0.087, 0.135)], with 63% of all individuals captured in only one trap night during a  
309 session, and 84% captured in only one or two trap nights. However, as expected for *Peromyscus*,  
310 average recapture probability increased sharply [posterior median odds ratio, odds of being  
311 captured on a given trap night for an individual captured the previous trap night divided by odds  
312 for an individual not captured the previous trap night, = 2.72 (2.39, 3.10)]. Posterior median  
313 abundance estimates ranged from 0–290 mice per grid per session ( $\bar{x}$  = 38.0, median = 21.0).  
314 Based on the standard deviation and mean of the 30,000 posterior abundance samples for the 198  
315 trap sessions, the median coefficient of variation (CV) within posterior abundance samples was  
316 25% (range 5–162%; all sessions with CVs >35% were sessions with 5 or fewer individuals  
317 captured).

318 Both uneven-aged and even-aged management systems increased *Peromyscus* abundance  
319 relative to no-harvest management (Table 2, Fig. 2). Based on the  $N_{posterior\_median}$  negative  
320 binomial model analysis, across the nine post-treatment sampling years the estimated average  
321 effect of uneven-aged management was to increase *Peromyscus* expected abundance by 73%  
322 compared to no-harvest management [UA vs NH: posterior median = 1.73; 95% credible interval  
323 = (1.11, 2.66); a value of 1.0 would correspond to no effect on abundance]. The estimated  
324 average effect of even-aged management was an 84% increase in expected abundance compared  
325 to no-harvest management ([EA vs. NH: 1.84 (1.09, 3.00)]. There was not a detectable difference  
326 between the two active management systems (EA vs UA: 1.07 (0.64, 1.72)]. Incorporating mark-



327 recapture estimation uncertainty increased overall uncertainty about treatment effects in terms of  
328 credible interval widths [Table 2; Fig. 2; average overall proportional effect of treatments based  
329 on  $N_{posterior\_sample}$  analysis which incorporated mark-recapture estimation uncertainty: UA vs NH:  
330 1.70 (1.01, 2.84); EA vs. NH: 1.80 (1.00, 3.18); EA vs UA: 1.06 (0.59, 1.85)].

331



332

333 Figure 1. Estimated abundances of *Peromyscus* on MOFEP small mammal grids in the Missouri  
 334 Ozarks for 11 sampling years during 1994–2014. Each panel corresponds to a single block × year  
 335 combination, with three sites per block (NH = no-harvest management UA = uneven-aged  
 336 management; EA = even-aged management) and two trap grids per site. Closed symbols are  
 337 median estimates from MCMC-estimated posterior distributions for each abundance parameter  
 338 from Bayesian closed-population mark-recapture modeling; error bars are 0.95 credible intervals  
 339 based on the (0.025, 0.975 percentiles) of the MCMC posterior samples. Open circles are the  
 340 number of unique *Peromyscus* individuals captured during each trapping session. Years 1994–  
 341 1995 were pre-treatment years; the first and second management entries occurred in 1996 and  
 342 2011.

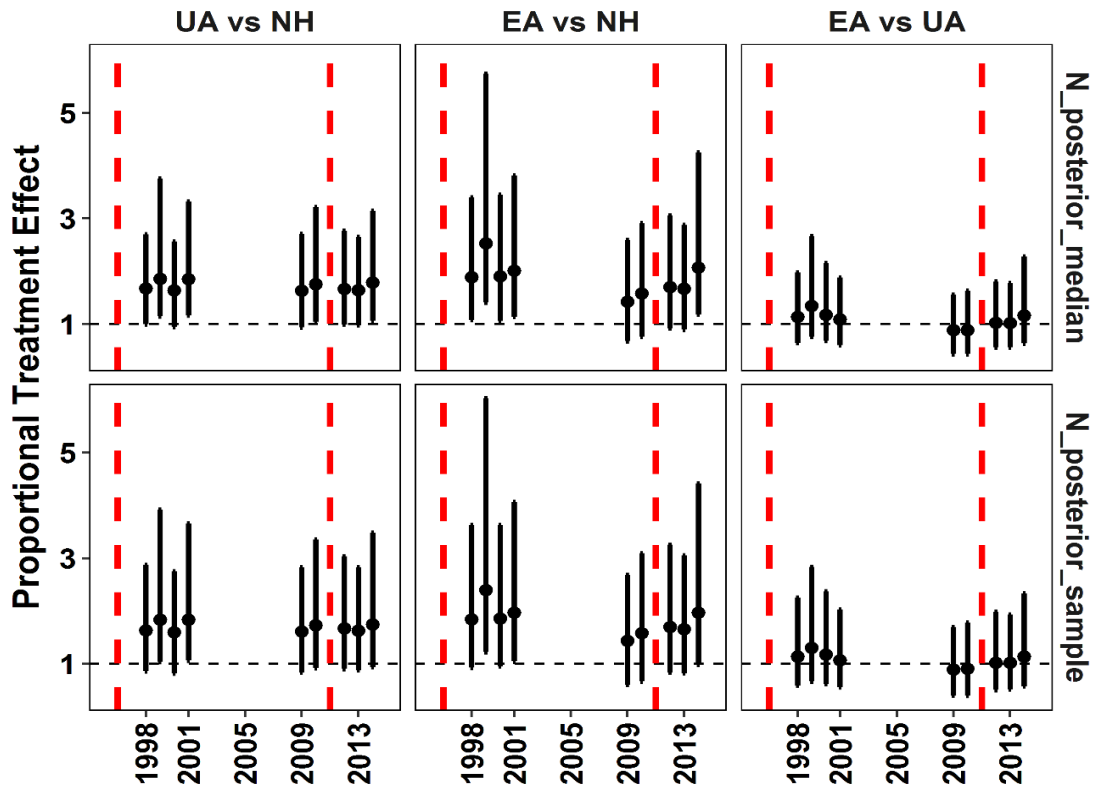
343 Table 2. Summaries of posterior distributions (median and 95% credible interval) for parameters  
 344 in Bayesian mixed effects model of *Peromyscus* expected abundance across 11 sampling years in  
 345 the MOFEP study. For the  $N_{posterior\_median}$  analysis, the negative binomial model was fit to  
 346 posterior median values of MCMC samples of abundance from mark-recapture estimation. For  
 347 the  $N_{posterior\_sample}$  analysis, we fit the negative binomial model to each of 3,000 abundance  
 348 vectors from the mark-recapture MCMC estimation, then pooled posterior samples for each  
 349 model parameter, with resulting credible intervals incorporating mark-recapture estimation  
 350 uncertainty. All parameters except  $r$  are log-scale effects; see Eq. 1 in Appendix.

351

| Parameter            | $N_{posterior\_median}$ | $N_{posterior\_sample}$ |
|----------------------|-------------------------|-------------------------|
| $B_0$                | 3.01 (2.05, 3.96)       | 3.11 (2.14, 4.09)       |
| $B\_block2$          | -0.41 (-0.96, 0.13)     | -0.44 (-1.07, 0.19)     |
| $B\_block3$          | -0.94 (-1.48, -0.42)    | -0.94 (-1.58, -0.32)    |
| $B\_pre$             | 0.01 (0.00, 0.01)       | 0.01 (0.00, 0.01)       |
| $B\_UA_{ave}$        | 0.55 (0.10, 0.98)       | 0.53 (0.01, 1.04)       |
| $B\_EA_{ave}$        | 0.61 (0.09, 1.10)       | 0.58 (-0.01, 1.15)      |
| $\sigma_{site}$      | 0.15 (0.01, 0.53)       | 0.13 (0.01, 0.66)       |
| $\sigma_{year}$      | 1.04 (0.54, 1.93)       | 0.93 (0.49, 1.92)       |
| $\sigma_{blockyear}$ | 0.38 (0.21, 0.60)       | 0.38 (0.18, 0.68)       |
| $\sigma_{UA\_year}$  | 0.18 (0.01, 0.55)       | 0.17 (0.01, 0.63)       |
| $\sigma_{EA\_year}$  | 0.34 (0.02, 0.83)       | 0.30 (0.02, 0.99)       |
| $r$                  | 3.66 (2.71, 4.83)       | 3.00 (2.18, 4.18)       |

352

353



354

355 Figure 2. Estimated proportional effects of MOFEP treatments on *Peromyscus* expected  
 356 abundance by sampling year. Values are posterior median and 95% credible interval for each  
 357 parameter from negative binomial mixed-effects model contrasting pairs of treatments by year  
 358 and analysis (NH = no-harvest management, UA = uneven-aged management, EA = even-aged  
 359 management). Upper row summarizes results from analysis that does not incorporate mark-  
 360 recapture estimation uncertainty ( $N_{posterior\_median}$  analysis which analyzed posterior median mark-  
 361 recapture abundance estimates for each trap session); bottom row summarizes results for  
 362 alternative analysis incorporating mark-recapture estimation uncertainty ( $N_{posterior\_sample}$  pooled  
 363 replicate analyses of individual samples from the posterior distribution of mark-recapture  
 364 abundance estimates). Vertical dashed lines indicate harvest treatment entries in 1996 and 2011;

365 horizontal dashed line is given for reference at 1.0 (proportional effect of 1.0 = no difference  
366 between treatments).

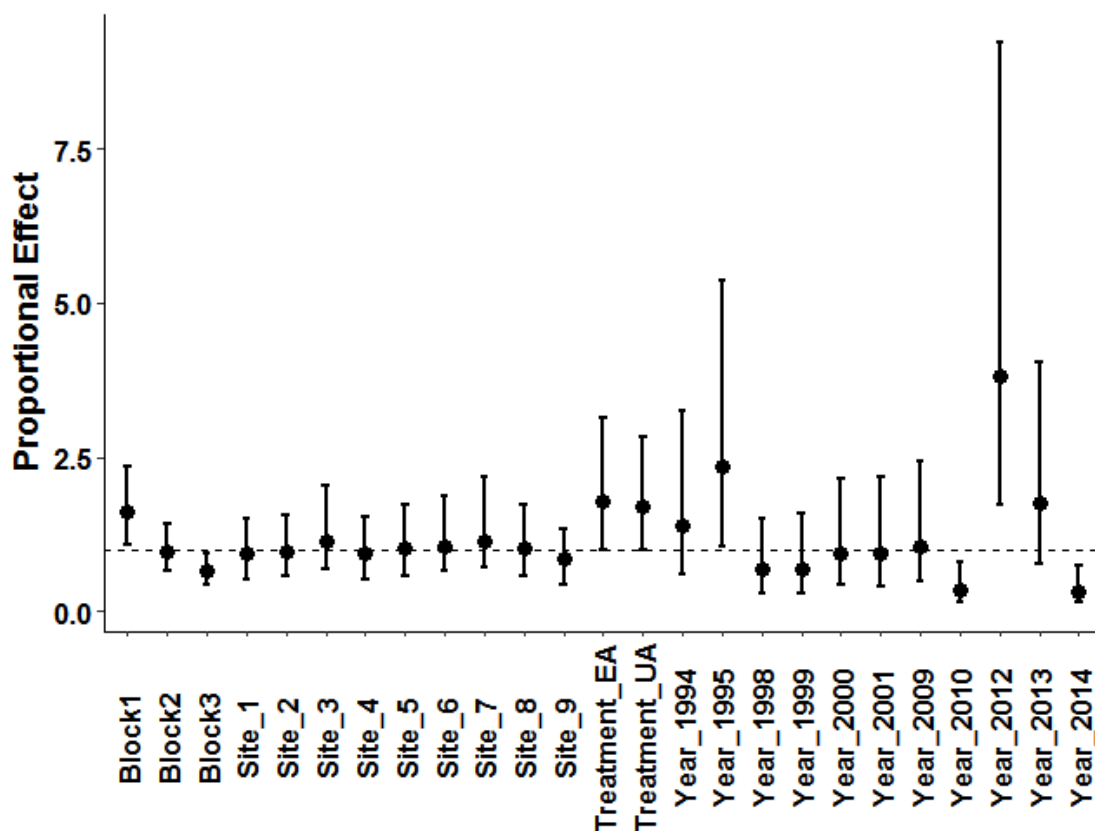
367 We observed upward shifts in yearly posterior distributions for even-aged treatment  
368 effects in 1999 and 2014, vs. potentially reduced effect of even-aged management in Years 13–  
369 14 after the first entry. This pattern suggested potential dissipation of the initial treatment effects  
370 followed by a return in magnitude after the second entry (Fig. 2). However, these were not  
371 conclusive patterns. Variance components capturing yearly variation in treatment effects had  
372 small estimated values (Table 2). Associated posterior medians and credible intervals for  
373 estimated deviations of year-specific treatment effects from the overall average for each  
374 treatment ( $b_{UA_y}$ ,  $b_{EA_y}$  in Appendix Eq. 2) indicated that none of the year-specific effects  
375 differed conclusively from the overall post-treatment average effect of each treatment.

376 Uneven-aged and even-aged management had large effects on expected abundance  
377 compared to other within-block persistent site effects (Fig. 3). Estimated persistent differences  
378 among blocks were similar to or greater than estimated effects of treatments. For example,  
379 expected *Peromyscus* abundance in Block 1 was estimated to be 2.5 (1.28, 4.73) times higher  
380 than in Block 3 on average. However, during several of the 11 sampling years, estimated area-  
381 wide yearly deviations from the multi-year average appeared to have stronger effects on  
382 expected abundance than block or treatment effects (Fig. 3). Contrasting the years of highest  
383 (975 mice) vs. lowest (102 mice) numbers of *Peromyscus* captured across all sites, expected  
384 abundance in 2012 was estimated to be 11.22 (4.14, 27.00) times higher than expected  
385 abundance in 2010.

386 During 1994–2014 no systematic log-linear long-term trend was evident for any  
387 treatment [proportional change in expected abundance per year: NH = 0.98 (0.89, 1.06), UA =  
388 1.00 (0.92, 1.10), EA = 1.00 (0.91, 1.09); value of 1.0 corresponds to no trend] nor across all  
389 study sites [refitting model to incorporate a single trend parameter common to all three

390 treatments, the yearly proportional change was 0.99 (0.91, 1.08)]. This analysis reinforced results  
391 from the yearly treatment-effects analysis, as both analyses indicated no detectable pattern of  
392 increasing divergence among treatments after two management entries, at least in terms of  
393 expected *Peromyscus* abundance. However, as the wide credible intervals summarize, high  
394 system-wide yearly variation produced high uncertainty about the existence of trends in  
395 *Peromyscus* abundance during the first 20 years of MOFEP.

396



397

398 Figure 3. Comparison of MOFEP treatment effects on *Peromyscus* expected abundance vs.  
 399 background spatial (block and site within block) and year effects. Values are estimated  
 400 proportional effects (posterior median and 95% credible interval) of harvest treatments (UA =  
 401 uneven-aged management, EA = even-aged management, relative to no harvest management) vs.  
 402 block-, site- and year-specific effects (deviations from long-term, system-wide average expected  
 403 abundance) from negative binomial mixed effects modeling of expected abundance, using  
 404 posterior median mark-recapture abundance as the response variable. Horizontal line at 1.0  
 405 indicates no effect; effects strengthen with increasing distance above or below 1.0.



406

407 **4. Discussion**

408 Both uneven- and even-aged management treatments increased *Peromyscus* abundance  
409 compared to no-harvest management. These increases were detectable shortly after the first entry  
410 and persisted through Year 18 post-treatment. A positive effect of treatments is unsurprising  
411 given results of past studies and MOFEP treatment effects on *Peromyscus* habitat attributes.  
412 Although *P. leucopus* sometimes declines in larger clearcut openings (Kellner et al., 2013;  
413 Kirkland, 1990), both *P. leucopus* and *P. maniculatus* are considered habitat and dietary  
414 generalists (Adler and Wilson, 1987; Cramer; 2014; Olsen et al., 2000; Seamon and Adler, 1996)  
415 that often respond positively to higher levels of ground cover, soft and hard mast, other seeds,  
416 insects, overall vegetation structural complexity (Fisher and Wilkinson, 2005; Kellner et al.,  
417 2013; Perry and Thill, 2005), and, in some cases, volume of down logs (Lee, 2004; Loeb, 1999;  
418 Manning and Edge, 2004; Urban and Swihart, 2011; but see also Bowman et al., 2000;  
419 Greenberg et al., 2006; Craig et al., 2006). At the site level, both uneven-aged and even-aged  
420 management increased ground-level cover of herbaceous vegetation and woody vines; in clearcut  
421 stands, average ground cover increased by 41% (absolute change) from pre-treatment to Years  
422 3–4 post-treatment (Grabner and Zenner, 2002; Zenner et al., 2006). Treatments also affected  
423 food and cover resources through increased berry production (Elizabeth Olson, MDC,  
424 unpublished data), development of high levels of small woody stem density from post-harvest  
425 stump sprouting (Kabrick et al., 2002), and addition of large amounts of woody debris to the  
426 forest floor of harvested areas. While the even-aged treatment reduced red oak acorn crops  
427 during the first 14 years post-treatment (Olson et al., 2015), the degree of reduction at the site  
428 level appeared minor compared to the magnitude of year-to-year variations in total acorn crops.

429 From the standpoint of MDC forest management on state lands, the observed effects of  
430 MOFEP treatments on *Peromyscus* abundance to date fit into an overall desirable pattern of  
431 responses by the vertebrate community, with no alarmingly negative effects observed for small  
432 mammals in this study or for amphibians, reptiles, or birds in other MOFEP studies (Kendrick et  
433 al., 2015; Rota et al., 2017; Wolf et al., 2016). For *Peromyscus*, treatment effects are not trivial,  
434 in that credible intervals indicate that uneven-aged and even-aged management each likely  
435 increase expected abundance by 50 to >100% compared to no-harvest management. Large  
436 changes in deermouse abundance could affect numerous other community attributes and  
437 processes such as vegetation demography and composition (Bricker et al., 2010; Gashwiler,  
438 1970a; Ostfeld et al., 1997; Tallmon et al., 2003; Zwolak et al., 2010), nest predation (Schmidt et  
439 al., 2001), predator populations (Jensen et al., 2012), invertebrate composition and abundance  
440 (Elkington et al., 1996; Jones et al., 1998), and transmission of parasites and diseases (e.g.  
441 Calisher et al., 2011; Ostfeld et al., 2006). Still, treatment effects on *Peromyscus* abundance are  
442 comparable in magnitude to the difference among MOFEP study blocks, and perhaps an order of  
443 magnitude less than the area-wide difference between years of peak vs. lowest abundance. At  
444 least under current conditions, there seems to be little risk that any MOFEP management  
445 alternative will drive *Peromyscus* abundance beyond its background range of spatial-temporal  
446 variability.

447 We observed relatively consistent effects of uneven-aged and even-aged management  
448 within groups of sampling years. This pattern is in line with Fantz and Renken (2005), who did  
449 not detect strong year-to-year variation in treatment effects during Years 2–5 post-treatment.  
450 However, less clear is why we did not detect conclusive variation in treatment effects among the  
451 three post-treatment groups of sampling years. Given rapid development of a dense sapling

452 midstory in openings created by MOFEP harvests (Good et al., 2017; Jensen and Kabrick, 2008;  
453 Kabrick et al., 2002), the pulse of ground-level resources observed initially after disturbance  
454 might have been expected to dissipate by Years 13–14 after the first entry as understory light  
455 levels declined. Yet, while berry production in Years 13–14 returned to baseline conditions  
456 comparable to pre-treatment levels, average graminoid cover of uneven-aged and even-aged  
457 treatment sites remained higher in Year 14 than in pre-treatment sampling (Elizabeth Olson,  
458 MDC, unpublished data). Increases in abundance of down logs due to thinning and harvest  
459 during the first entry likely persisted through the next two decades, with such increases  
460 potentially important given that pre-treatment MOFEP sites were near a predicted low point in  
461 the U-shaped pattern of deadwood volume vs. stand age in hardwood-dominated forests of the  
462 central U.S. (Spetich et al., 1999).

463         With positive effects of the first management entries on *Peromyscus* populations  
464 persisting, it is unclear why the second MOFEP entry did not produce a detectable amplification  
465 of treatment effects. Any initial dissipation of treatment effects in Years 13–14 may have been  
466 reversed by an additional round of positive effects from the second management entry in Year  
467 15. Another potential factor is that MOFEP small mammal grids within uneven-aged and even-  
468 aged treatment sites received heterogeneous exposure to management actions within and across  
469 individual entries. For example, in even-aged treatment sites, sampling grids had more overlap  
470 overall with stands clearcut harvested in the first entry than with clearcut areas in the second  
471 entry, while overlap with intermediate thinning areas was higher in the second entry. Lack of  
472 conclusive differences in treatment effects across the 11 post-treatment sampling years could  
473 also reflect statistical imprecision associated with the level of replication feasible in this  
474 operational experiment and the high temporal variability of *Peromyscus* populations. As more

475 entries and rounds of sampling occur, MOFEP researchers will have increased ability to assess  
476 temporal and spatial patterns in effects of individual entries. There will also be increased ability  
477 to integrate data across core research areas (e.g. data on understory vegetation and small  
478 mammal abundance) so as to better understand mechanisms driving responses to treatments.

479         For MOFEP's overarching focus on long-term, landscape-scale effects of the three  
480 management systems, assessing short-term responses to individual entries is useful mainly as a  
481 step in understanding and predicting potential broader scale effects. Based on results to date from  
482 MOFEP studies of tree species composition and stand dynamics, currently a major overall  
483 question of MOFEP is how the three alternative management systems will interact with other  
484 factors affecting forest composition across many portions of the central U.S. (Olson et al., 2017).  
485 One important uncertainty is whether maples (particularly *Acer rubrum* and *A. saccharum*) will  
486 become an important overstory species on any MOFEP sites. Although maples historically were  
487 likely absent from upland forests of the Missouri Ozarks (Guyette et al., 2007; Hanberry et al.,  
488 2014; Olson et al., 2017), over the last 20 years maples have become a major component of the  
489 MOFEP seedling and sapling size classes (Olson et al., 2014; Olson et al., 2017). Still, while  
490 replacement of oaks by maples and other shade-tolerant species is an ongoing transition  
491 elsewhere in the eastern U.S. (Nowacki and Abrams, 2008; Rogers et al., 2008; Shotola et al.,  
492 1992) low-quality soils and frequent droughty conditions of the Missouri Ozarks may inhibit  
493 recruitment of maples to the overstory (Olson et al., 2014). To the extent such recruitment  
494 occurs, managers will have greater ability to affect the relative abundance of maples under  
495 uneven-aged and even-aged systems compared to no-harvest management.

496         A less speculative pathway of divergence among MOFEP treatments is in the species  
497 composition of oaks, specifically the relative numbers of red oak species (with black oak, *Q.*

498 *velutina*, and scarlet oak, *Q. coccinea* most abundant on MOFEP sites) vs. white oak species  
499 (particularly white oak, *Q. alba*, and post oak, *Q. stellata*) (Jensen and Kabrick, 2008). On no-  
500 harvest sites, oak decline and resulting senescence of the shorter-lived red oaks has shifted  
501 overstory dominance to white oaks (Olson et al., 2017). With current low densities of shade-  
502 intolerant and intermediate-tolerance red oak species as sapling or midstory trees, replacement  
503 by white oaks and other species on no-harvest sites likely will continue. The experiment's  
504 uneven-aged management treatment may not maintain red oaks as a major species group unless  
505 harvests reduce overstory densities and increase light levels to a greater degree than in single-tree  
506 selection harvests of the first entry (Fan et al., 2015; Jensen and Kabrick, 2008). However, given  
507 observed successful regeneration in clearcut openings, higher site-level abundance of red oaks  
508 may be maintained under even-aged management (Fan et al., 2015; Jensen and Kabrick, 2008).

509         Shifting dominance of white oaks vs. red oaks and potential addition of maples to the  
510 overstory assemblage are important factors for considering future patterns of abundance of  
511 *Peromyscus* among the MOFEP treatments. Abundance of hard mast can strongly affect  
512 *Peromyscus* populations (Clotfelter et al., 2007; McCracken et al., 1999; McShea, 2000, Ostfeld  
513 et al., 1996; Schnurr et al., 2002; Wolff, 1996). Even if combined density of red and white oaks  
514 does not decline, replacement of red oaks by white oaks could reduce size and year-to-year  
515 consistency of overall acorn crops (Greenberg and Parresol, 2002; Greenberg et al., 2014; Olson  
516 et al., 2015). Moreover, acorns from the two groups may not have interchangeable value. Higher  
517 tannic acid levels of red oak acorns may reduce their palatability, but the resulting slower rate of  
518 rotting, along with their pattern of overwintering before germinating, also may make red oak  
519 acorns a more reliable over-winter food source (Kirkpatrick and Pekins, 2002; Olson, 1974;  
520 Wang et al., 2009).

521           However, there is high uncertainty regarding the potential responses of *Peromyscus*  
522 populations to changes in forest composition and hard mast crops of MOFEP sites. During first  
523 15 years post-treatment, even-aged MOFEP treatments reduced overall acorn crop size  
524 moderately, with further reduction likely during the next few entries until acorn production  
525 begins by cohorts resulting from early entries (Olson et al., 2015). Based on our results, this  
526 decrease either was not significant enough to affect *Peromyscus* spring abundances or was  
527 counterbalanced by other effects of the initial MOFEP management entries. Links between  
528 *Peromyscus* abundance and acorn crops, particularly of red oak species, are strongest at more  
529 northern latitudes, with decoupling of *Peromyscus* abundance and acorns crops in some areas  
530 further south, conjecturally due a more diverse food base (Gillen and Hellgren, 2013; Wang et  
531 al., 2009). In the southern Central Hardwoods region, *Peromyscus* abundance may not show a  
532 strong relationship with stand-level density of hard mast species or with hard mast biomass  
533 (Gillen and Hellgren, 2013). Maple seeds are also consumed by *Peromyscus* (e.g. Cramer, 2014)  
534 and the magnitude of maple seed crops may contribute to *Peromyscus* population changes  
535 (McCracken et al., 1999; but see Schnurr et al., 2002). Speculatively, this additional food  
536 resource could compensate for some reduction in hard mast or even further diversify the food  
537 base.

538

## 539 **5. Conclusions**

540 Across studies of forest floor small mammal community responses to disturbances, the most  
541 consistently observed pattern is the one we observed with MOFEP *Peromyscus*: generalist  
542 species remaining numerically dominant across successional states, frequently with increased  
543 abundance after disturbance (Bogdziewicz and Zwolak, 2014; Kirkland, 1990). In light of

544 *Peromyscus* responses so far to MOFEP treatments and expected positive effects of periodic  
545 management entries on important food and cover resources, uneven-aged and even-aged  
546 management likely will continue to maintain increased abundance of *Peromyscus* compared to  
547 no-harvest management. Whether this difference changes over time or whether divergence in  
548 abundance under uneven-aged vs. even-aged management occurs may depend partly on the  
549 sensitivity of these *Peromyscus* populations to differential changes in overstory composition,  
550 particularly in terms of the comparative densities of red oaks, white oaks, and maples (Gillen and  
551 Helgren, 2013). In addition, although *Peromyscus* populations may respond positively to  
552 increased habitat heterogeneity and structural complexity (Carey and Johnson, 1995), an open  
553 question with broad relevance to forest management is the relative importance of higher within-  
554 stand vertical heterogeneity expected under long-term application of uneven-aged management  
555 (but see Angers et al., 2005) vs. higher between-stand heterogeneity and availability of larger  
556 early successional patches produced by even-aged management (e.g. Holmes et al., 2012;  
557 Joelsson et al., 2018; Schall et al., 2017; Thompson et al., 1995).

558         Our statements of general expectations are not intended to downplay high uncertainty  
559 about potential changes in MOFEP forests and wildlife communities over the next several  
560 decades. A unique value of long-term studies is the chance to iteratively improve understanding  
561 of a system, quantify unexpected changes, and assess effects of infrequent and rare events  
562 (Hobbie et al., 2003; Lindenmayer and Likens, 2010:8; Turner et al., 1998). As additional years  
563 of data are collected, more insights will be possible about the relative magnitude of treatment  
564 effects vs. system-wide year-to-year variation, and about interactions between harvest treatments  
565 and other factors (e.g. mast crops; weather) potentially driving temporal variation in *Peromyscus*  
566 abundance. Understanding drivers of high year to year variation will increase our ability to detect

567 and explain differential long-term trends in abundance (Urquhart et al., 1998) and forecast future  
568 potential changes. The MOFEP experiment has an especially long time horizon, but has reached  
569 a point of providing a unique understanding of cumulative and long-term forestry impacts at a  
570 landscape scale.

571

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578

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584

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881

## 882 **Appendix**

### 883 **A.1. Analysis overview**

884 To examine effects of MOFEP experimental treatments (i.e. alternative forest management  
885 systems) on *Peromyscus* abundance, we first attempted a Bayesian hierarchical modeling  
886 approach following Schofield and Barker (2014) and Converse and Royle (2012), which  
887 integrates modeling of the observation process (via mark-recapture estimation) and the  
888 underlying ecological process of interest (variability in abundance across sites and years). For  
889 such integrated modeling of abundance in mark-recapture studies, Converse and Royle (2012)  
890 outlined Markov Chain Monte Carlo estimation (MCMC) via parameter-expanded data-  
891 augmentation, with abundance as a derived parameter, while Schofield and Barker (2014)  
892 outlined a trans-dimensional MCMC approach with explicit inclusion of abundance as a model  
893 parameter. In extensive pilot analyses, regardless of which approach we used, computer  
894 processing time and extremely slow model convergence made the analysis unfeasible using  
895 JAGS and BUGS (WinBUGS, OpenBUGS) when we attempted to model more than a few years  
896 of data at a time. We believe this issue was due to the large number of mice captured (3,871) and  
897 trap sessions (198) conducted in MOFEP, possibly exacerbated by relatively low capture  
898 probabilities, as we have used these approaches successfully in other studies with smaller multi-  
899 session mark-recapture data sets for *Peromyscus* (R. A. Gitzen, unpublished data; see also  
900 Sollmann et al., 2015). Therefore, we performed a two-stage analysis, first estimating abundance  
901 via mark-recapture modeling, then modeling variation in abundance as a function of treatment  
902 and other factors.

903

## 904 **A.2. Bayesian Mark-recapture Modeling**

905 We used a zero-augmentation approach to Bayesian closed-population mark-recapture modeling  
906 (Kéry and Schaub, 2012; Royle and Dorazio, 2008; Royle; et al., 2007). Each session's observed  
907 capture histories were augmented with additional all-zero capture histories. The 198 sets of  
908 resulting capture histories were combined into a single response-variable matrix ( $\mathbf{C}$ ) for unified  
909 mark-recapture analysis. With the general zero-augmented approach, each capture history is  
910 associated with a partially latent session "occupancy" parameter denoting whether the capture  
911 history is for an individual animal actually present during the session or represents a non-existent  
912 individual. That is, the approach formulates the abundance-analysis problem as that of estimating  
913 how many of the augmented all-zero capture histories for a session correspond to individuals  
914 present but not captured. In each MCMC iteration, the abundance estimate for a session was the  
915 sum of the number of individuals actually captured plus the number estimated to be present but  
916 not captured.

917 The primary detectability model we used was a form of the general model  $M_{tb}$  (Otis et al.,  
918 1978) incorporating within-session variability in capture probabilities due to temporal and  
919 behavioral (i.e. response to prior capture) effects (Eq. 1).

920



921 Eq. 1

$$\text{logit}(p_{i,n}) = Lp\_mu + lp\_blockyear_{by[i]} + lp\_blockyearnight_{by[i],n} + lp\_session_{bsgy[i]} + \text{Recap}_{i,n} * (Lrp\_mu + lrp\_session_{bsgy[i]})$$

$$C_{i,n} \sim \text{Bernoulli}(p_{i,n} * Z_i)$$

922  $Z_i \sim \text{Bernoulli}(\Omega_{ybsg})$

$$lp\_blockyear_{by} \sim \text{Normal}(0, \sigma_{lp\_blockyear})$$

$$lp\_blockyearnight_{byn} \sim \text{Normal}(0, \sigma_{lp\_blockyearnight})$$

$$lp\_session_{bsgy} \sim \text{Normal}(0, \sigma_{lp\_session})$$

$$lrp\_session_{bsgy} \sim \text{Normal}(0, \sigma_{lrp\_session})$$

923 Here, the capture history value  $C_{i,n}$  equaled 1 if individual  $i$  was captured in trap night  $n$  of the  
 924 trap session of block  $b$ , site  $s$ , grid  $g$ , and year  $y$ , and equaled 0 otherwise. The session occupancy  
 925 parameter,  $Z_i$ , equaled 1 for captured individuals and other individuals estimated to be present  
 926 during the session but not captured, and equaled zero otherwise. As is standard with the zero-  
 927 augmented approach,  $Z_i$  was modeled as a Bernoulli outcome with session occupancy probability  
 928  $\Omega_{bsgy}$ , with the latter given a *Uniform*(0,1) prior distribution. Logit-scale detectability for  
 929 individual  $i$  in trap night  $n$  of the session was modeled as an additive function of an overall logit-  
 930 scale fixed-effect mean ( $Lp\_mu$ ), a block  $\times$  year random effect ( $lp\_blockyear$ ), a nested block  $\times$   
 931 year  $\times$  night random effect ( $lp\_blockyearnight$ ) allowing night-to-night variation within a  
 932 session, a nested session-specific random effect ( $lp\_session$ ) to allow additional grid-to-grid  
 933 variation within a block  $\times$  year combination, an overall fixed behavioral (recapture) effect  
 934 ( $Lrp\_mu$ ), and a session-specific random effect adjustment ( $lrp\_session$ ) to this average  
 935 recapture effect. The variable  $\text{Recap}_{i,n}$  equaled 1 if individual  $i$  was captured in the previous trap  
 936 night of the session, and equaled 0 otherwise. Logit-scale night-to-night variability in detection  
 937 probability within a session was constrained to be have homogenous effects on detectability  
 938 across the six grids sampled in block  $b$  during year  $y$ . This approach allowed within-session

939 variation but reduced model complexity. This approach was appropriate because the six grids  
940 within each block were trapped simultaneously each year, thus subject to parallel variation in  
941 weather, moon phase, etc.

942 In the Bayesian model, random effects standard deviation parameters were given separate  
943  $\text{abs}[Normal(\text{mean} = 0, \text{precision} = 0.1)]$  prior distributions, while the fixed-effect average  
944 recapture effect ( $Lrp\_mu$ ) was given a  $Student's\_t(\text{mean} = 0, \text{precision} = 0.16, \text{df} = 5)$  prior  
945 distribution. These were weakly informative prior distributions that avoided putting significant  
946 prior probability mass outside a liberally plausible range for each logit-scale parameter. Average  
947 probability of first capture was given a  $Uniform(0.0, 0.5)$  distribution and logit-transformed to  
948  $Lp\_mu$ ; its upper bound was constrained at 0.5 to speed convergence after preliminary modeling  
949 with a  $Uniform(0.0, 1.0)$  distribution indicated probability of  $\sim 1.0$  that the parameter was  $< 0.5$ .  
950 Therefore, constraining the range of the prior did not limit the resulting posterior distribution.

951 Posterior distributions were estimated with MCMC sampling using program JAGS and R  
952 package rjags (Plummer, 2016). Following an adaptive phase of 2500 samples and 105,000 burn-  
953 in samples, with convergence confirmed via traceplots and the Gelman-Rubin convergence  
954 diagnostic (Gelman and Rubin, 1992), the posterior distribution for each parameter was  
955 estimated with 30,000 samples (every 10<sup>th</sup> sample retained of 100,000 post-convergence samples  
956 for each of three chains). We estimated the posterior distribution for the average recapture odds  
957 ratio (odds of capture in trap night  $n$  if an individual was captured on the previous trap night /  
958 odds of capture if not captured on the previous trap night) by exponentiating ( $Lrp\_mu$ ) within  
959 each MCMC iteration. For this and all subsequent analyses in this manuscript, posterior  
960 distributions were summarized by the posterior median MCMC sample value for each parameter

961 and a 95% credible interval formed by taking the (0.025, 0.975) percentiles of the posterior  
962 samples.

963

### 964 **A.3. Modeling abundance of *Peromyscus***

965 Our second stage of analyses used these mark-recapture abundance posterior distributions to  
966 form response variables for modeling variation in abundance of *Peromyscus* across sites and  
967 years. Modeling focused on our objectives of estimating treatment effects, comparing the  
968 magnitude of treatment effects to background spatial and temporal variation in the system, and  
969 assessing evidence of long-term trends in abundance. For these three objectives, we examined  
970 three alternative forms of a general negative binomial log-linear mixed effects model. This  
971 allowed us to tailor the general model to each objective.

972

#### 973 **A.3.1. Estimating treatment effects on *Peromyscus* abundance**

974 We estimated overall and yearly site-level effects of the three MOFEP management systems on  
975 expected abundance ( $\lambda$ ), using estimated abundances by grid for the nine post-treatment years as  
976 the response variable and average pre-treatment (1994 and 1995) estimated abundances as a  
977 covariate (sensu Senn, 2006) (Eq. 2).

978

979 Eq. 2

$$\ln(\lambda_{bsgy}) = B_0 + B\_block2_{b=2} + B\_block3_{b=3} + B\_pre * \bar{N}_{pre,bsg} + \\ [B\_UA_{ave} + b\_UA_y] * UA_s + [B\_EA_{ave} + b\_EA_y] * EA_s + \\ b\_year_y + b\_blockyear_{by} + b\_site_s$$

$$N_{bsgy} \sim NegBinom(\lambda_{bsgy}, r)$$

980

$$b\_UA_y \sim Norm(0, \sigma_{UA\_year})$$

$$b\_EA_y \sim Norm(0, \sigma_{EA\_year})$$

$$b\_year_y \sim Norm(0, \sigma_{year})$$

$$b\_blockyear_{by} \sim Norm(0, \sigma_{blockyear})$$

$$b\_site_s \sim Norm(0, \sigma_{site})$$

981

982 Here,  $N_{bsgy}$  equaled grid-level abundance for grid  $g$  in block  $b$ , site  $s$ , and year  $y$ , grid  $g$ , limited to  
 983 the 162 post-treatment (1998–2014) trapping sessions;  $r$  designated the negative binomial  
 984 dispersion parameter; covariate  $\bar{N}_{pre,bsg}$  equaled average pre-treatment (1994–1995) abundance  
 985 for grid  $bsg$ ; and  $UA_s$  and  $EA_s$  indicated the experimental treatment to which site  $s$  was assigned.  
 986 The log-linear model included block effects (incorporated as a fixed effect to avoid estimating a  
 987 variance component based on only three blocks) and random site, year, and block  $\times$  year effects.  
 988 The year random effect was crossed with block and site effects, such that the year effect modeled  
 989 the component of year-to-year variation that was consistent across the study area, while the block  
 990 and site effects represented block- and site-identity effects that were persistent across years  
 991 (Urquhart et al., 1998). Other potential random effects were omitted to avoid further model  
 992 complexity when preliminary analyses indicated that the effects (e.g. persistent effects of grid;  
 993 site  $\times$  year grouping) were essentially zero or not estimable given other effects incorporated.

994           Log-scale effects of uneven-aged and even-aged management were modeled with fixed-  
995 effects parameters for the average effect of each harvest treatment relative to the no-harvest  
996 treatment ( $B_{UA_{ave}}$ ,  $B_{EA_{ave}}$ ) and additional random effects allowing for yearly variation in the  
997 effects of each treatment ( $b_{UA_y}$ ,  $b_{EA_y}$ ) for the nine post-treatment sampling years. For  
998 interpreting model estimates, posterior distributions for proportional effects of harvest treatments  
999 relative to the no-harvest treatment were estimated by exponentiating each posterior sample of  
1000 the log-scale overall and year-specific treatment effects; the same approach was used for all  
1001 subsequent analyses to transform log-scale additive effects into proportional effects. To compare  
1002 uneven-aged vs. even-aged management effects, we calculated posterior distributions for the  
1003 ratio of even-aged to uneven-aged proportional effects (ratios of average effects and of year-  
1004 specific effects).

1005           Posterior distributions for parameters in the negative binomial mixed effects model were  
1006 estimated with MCMC in Stan via R packages brms (Buerkner, 2017) and RStan (Stan  
1007 Development Team, 2016). We conducted two sets of analyses with the yearly treatment model.  
1008 First, we analyzed the single vector of posterior median abundance estimates from Bayesian  
1009 mark-recapture modeling; the pre-treatment covariate values were the average of the two pre-  
1010 treatment posterior median estimates for each grid. We estimated posterior distributions for this  
1011  $N_{posterior\_median}$  analysis using the default 4 chains in package brms, with 1,000 warm-up samples  
1012 and 1,000 retained samples per chain (4,000 total posterior samples retained). Convergence was  
1013 assessed as in the Bayesian mark-recapture analysis but far fewer samples were needed because  
1014 of high efficiency and rapid convergence in Stan.

1015           Although this analysis accounted for among-session variation in capture probabilities  
1016 because it used absolute abundance estimates, the analysis did not incorporate mark-recapture

1017 estimation uncertainty. To assess whether posterior uncertainty about model parameters  
1018 increased meaningfully when this mark-recapture estimation uncertainty was incorporated, we  
1019 performed a second analysis of the treatment-effects model ( $N_{posterior\_sample}$ ) using individual  
1020 samples from the 198 posterior distributions for session-specific abundance from mark-recapture  
1021 modeling. The Bayesian mark-recapture sampling produced 30,000 posterior abundance vectors,  
1022 each containing a sample vector of length 198. For each of 3,000 of these vectors (every 10<sup>th</sup>  
1023 multivariate sample), we used the posterior abundance vector as input data for the negative  
1024 binomial abundance model described above, with the pre-treatment average abundance for each  
1025 grid calculated using the relevant pre-treatment abundance values from that sample vector. Using  
1026 the brms package, we obtained 1,000 samples from the posterior distributions for the abundance  
1027 model parameters (a single MCMC chain with 1,000 warm-up samples and 4,000 posterior  
1028 samples thinned to retain every 4<sup>th</sup> value; initial analyses of multiple chains indicated  
1029 consistently adequate convergence after 1,000 warmup samples, and running one chain reduced  
1030 computer run time by several days). We then pooled these 400 sets of posterior samples of  
1031 negative binomial model parameters to obtain an overall posterior sample for each parameter of  
1032 length  $400 \times 1000 = 400,000$ , which incorporated uncertainty in the 198 abundance estimates.  
1033 For both the  $N_{posterior\_median}$  and  $N_{posterior\_sample}$  analyses, we used default prior distributions of the  
1034 brms package (Buerkner, 2017).

1035

### 1036 **A.3.2. Relative magnitude of treatment effects on *Peromyscus* abundance**

1037 To compare the relative magnitude of effects of uneven-aged and even-aged harvest management  
1038 on abundance vs. effects of background spatial and temporal variation in the MOFEP system, we  
1039 used posterior summaries for treatment effects from the above analysis. That analysis used the

1040 pre-treatment average abundance covariate to increase precision of treatment-effect estimates.  
1041 However, incorporating pre-treatment abundance as a covariate meant that year effects were  
1042 modeled based on (and estimated for) 9 rather than 11 years, and the model essentially  
1043 partitioned persistent spatial variation into a component explained by pre-treatment abundance  
1044 and components capturing any additional block and site effects not explained by pre-treatment  
1045 abundance. To better estimate background block, site, and year effects for comparison with  
1046 treatment effects, we ran a modified form of the  $N_{posterior\_median}$  analysis. The modified approach  
1047 included all 11 sampling years and omitted pre-treatment abundance as a covariate. We  
1048 calculated posterior summaries for block-, site- and year-specific proportional effects, where  
1049 each effect was a proportional change from the long-term, area-wide average expected  
1050 abundance. We visually compared estimated effects of year, block, and site effects with  
1051 estimated treatment effects from the  $N_{posterior\_median}$  analysis. The treatment-effects analyses  
1052 ( $N_{posterior\_median}$  vs.  $N_{posterior\_sample}$ ) indicated that incorporating estimation uncertainty increased  
1053 the width of posterior credible intervals somewhat (Table 2; Fig. 2), but not enough to affect our  
1054 interpretations of the general relative strength of different effects. Therefore, we did not conduct  
1055 time-intensive  $N_{posterior\_sample}$  analyses to incorporate estimation uncertainty for addressing this  
1056 objective.

1057

### 1058 **A.3.3. Trend analysis**

1059 The treatment-effects analysis examined average and year-specific relative differences among  
1060 management systems, but to avoid additional model complexity we did not include temporal  
1061 trend parameters in that model. To assess whether *Peromyscus* abundance was exhibiting

1062 system-wide or treatment-specific log-linear trends within the first 20 years of the MOFEP study,  
 1063 we analyzed a modified form of the negative binomial abundance models (Eq. 3).

1064

1065 *Eq. 3*

$$\ln(\lambda_{bsgy}) = B_0 + B\_block2_{b=2} + B\_block3_{b=3} + B_{Treatment(s)} * Year_y + b\_UA_y * UA_s + b\_EA_y * EA_s +$$

$$b\_year_y + b\_blockyear_{by} + b\_site_s$$

1066

$$N_{bsgy} \sim NegBinom(\lambda_{bsgy}, r)$$

1067 In this modified model,  $Year_y$  was a numeric covariate (scaled to be 0 for 1994);  $B_{treatment}$   
 1068 indicated a treatment-specific log-linear trend parameter allowing separate trends for no-harvest,  
 1069 uneven-aged, and even-aged management, respectively; and other parameters and random effects  
 1070 distributions were as described above. See, for example, Urquhart et al. (1998) for development  
 1071 of a general multi-site trend model in which year is included as both a numeric covariate for  
 1072 modeling systematic long-term trends and as a categorical random effect to capture additional  
 1073 yearly variation not accounted for by the systematic trend. In the above model, site- and year-  
 1074 specific treatment random effects modeled among-treatment differences apart from those  
 1075 captured by the log-linear trend effects. Using posterior median abundance estimates for 1994–  
 1076 2014 as input data, we estimated posterior distributions for the trend-model parameters using  
 1077 package brms as in previous  $N_{posterior\_median}$  analyses (i.e. four chains, with 4,000 total samples  
 1078 retained for inference). Posterior samples for log-scale trend parameters were exponentiated to  
 1079 estimate posterior distributions for proportional trends (e.g. value of 1.02 = 2% increase in  
 1080 expected abundance per year). Again, we did not conduct time-intensive  $N_{posterior\_sample}$  analyses  
 1081 to incorporate estimation uncertainty in trend modeling as it was apparent that minor increases in  
 1082 posterior uncertainty would not change conclusions from the  $N_{posterior\_median}$  trend analysis.



1083           With all abundance-modeling analyses, we did not explicitly account for correlation  
1084 among abundance estimates induced by unified mark-recapture modeling (sensu and Converse et  
1085 al., 2006; Skalski and Robson, 1992:153). However, we believe this had little or no effect on our  
1086 results. The primary grouping structure assumed for variation in capture probability among  
1087 sessions within the mark-recapture analysis was block  $\times$  year variation. However, raw capture  
1088 counts exhibited high variation among blocks, years, and block  $\times$  year groups, imposing a strong  
1089 correlation in capture counts in sessions within groups independent of mark-recapture modeling.  
1090 Unified mark-recapture modeling appeared to contribute little to this already strong structure,  
1091 based on preliminary comparisons of the block  $\times$  year variance component estimates from  
1092 negative binomial treatment-effects abundance analyses using raw capture counts vs. those using  
1093 posterior median abundance estimates. Incorporation of block, year, and block  $\times$  year effects in  
1094 the negative binomial abundance modeling therefore addressed both high natural spatial-  
1095 temporal within-group correlation and additional within-group correlation in abundance  
1096 estimates induced by the unified mark-recapture modeling. Independent estimation of abundance  
1097 for each session was not feasible given the large number of trap sessions with few individual  
1098 animals captured (e.g. 51 of 198 sessions had 5 or fewer mice captured).