



Original Investigation

Investigating the effects of forest structure on the small mammal community in frequent-fire coniferous forests using capture-recapture models for stratified populations

Rahel Sollmann^{a,*},¹, Angela M. White^b,¹, Beth Gardner^a, Patricia N. Manley^b

^a North Carolina State University, Department of Forestry and Environmental Resources, Fisheries, Wildlife and Conservation Biology Program, Raleigh, NC, United States

^b US Forest Service, Pacific Southwest Research Station, Davis, CA, United States

ARTICLE INFO

Article history:

Received 3 November 2014

Accepted 12 March 2015

Handled by Adriano Martinoli

Available online 20 March 2015

Keywords:

Abundance

Distribution

Disturbance regime

Live trapping

Forest management

ABSTRACT

Small mammals comprise an important component of forest vertebrate communities. Our understanding of how small mammals use forested habitat has relied heavily on studies in forest systems not naturally prone to frequent disturbances. Small mammal populations that evolved in frequent-fire forests, however, may be less restricted to specific habitat conditions due to the instability of these resources in time and space. We investigate how canopy cover and the volume of coarse woody debris (CWD), covariates that are considered important for small mammals, impact abundance and body mass of eight small mammal species. Based on live-trapping data collected across 23 sites over three years in a frequent fire forest in the Sierra Nevada we apply capture-recapture models for stratified populations, a statistically rigorous, rarely used framework that allows joint modeling of detection, abundance and its response to covariates. Canopy cover had a strong negative association with the abundance of yellow-pine chipmunks and California ground squirrels, and a strong positive association with deer mice. CWD had a strong negative association with the abundance of golden-mantled ground squirrels, yellow-pine and long-eared chipmunks, and a strong positive association with deer mice. Whereas canopy cover influenced abundance and body mass similarly, CWD had a positive association with body mass and a negative association with abundance in some species. These patterns could arise if suitable habitat is monopolized by socially dominant individuals. Despite these habitat associations, the small mammal community in our study was dynamic and diverse, with spatial and temporal variation in dominant species suggesting that species were flexible in their use of habitat. This study suggests that it is important to understand the disturbance regimes when investigating habitat requirements, coexistence and evolutionary ecology of small mammal species.

© 2015 Deutsche Gesellschaft für Säugetierkunde. Published by Elsevier GmbH. All rights reserved.

Introduction

Small mammals comprise an important component of the vertebrate biomass and diversity in coniferous forests (Lawlor, 2003). They influence forest vegetation structure through dispersal of seeds and hypogeous fungi (Carey et al., 1999; Price and Jenkins, 1987; Pyare and Longland, 2001) and are an important food source for forest carnivores (Smith et al., 1999; Zielinski et al., 1999). The impact of forest management practices has dominated the

ecological context of studies on forest-dwelling small mammals (Bagne and Finch, 2010; Greenberg et al., 2006; Monroe and Converse, 2006). One overriding theme of these studies is that human-induced disturbance to these systems has led to a decrease in old-growth forest specialists such as voles and northern flying squirrel (Carey and Johnson, 1995; Fauteux et al., 2013; Lemaître et al., 2010; Smith, 2007). Whereas specialists are expected to evolve in relatively stable or homogeneous environments, niche theory predicts that heterogeneous environments or environments with frequent disturbances will be dominated by generalists (Devictor et al., 2008; Kassen, 2002).

The coniferous forests of the western United States were historically exposed to regular fires. A century of fire suppression, in combination with intensive timber harvest, has drastically altered forest structure and disturbance regime. Where large overstory trees were removed during early timber harvests, subsequent fire

* Corresponding author at: North Carolina State University, Department of Forestry and Environmental Resources, Campus Box 8008, Raleigh, NC 27695, United States. Tel.: +1 919 7063658.

E-mail address: rsollma@ncsu.edu (R. Sollmann).

¹ Both authors contributed equally to the manuscript.

suppression has resulted in relatively homogeneous, even-aged forest stands with denser canopies (Knapp et al., 2013). Compared to more mesic forests, studies of small mammals in high-frequency fire forests are few and have been largely restricted to the more homogeneous forests of the interior US (Stephens et al., 2012, 2014). In addition, because these studies were usually conducted shortly after mechanical thinning or prescribed fire, it has been difficult to ascertain whether wildlife responses are a consequence of disturbance or changed habitat structure. Therefore, the spatial and ecological context of previous studies limits inferences about habitat associations and the impact of forest management on small mammals that evolved in forests with frequent disturbance regimes.

The presence and abundance of small mammals in forested habitats is often correlated with habitat structure (Hallett et al., 2003; Johnston and Anthony, 2008; Lawlor, 2003; Naxara et al., 2009). Canopy cover, for example, influences the availability of resources on the forest floor, and small mammals are frequently positively associated with more open forests (e.g., Bellows et al., 2001; Greenberg et al., 2006), which are characterized by denser, more complex understory vegetation (Knapp et al., 2013). Downed coarse woody debris (CWD) is also an important habitat feature, as it supports insects and fungi and provides nesting habitat and cover from predators (e.g., Ecke et al., 2002; Fauteux et al., 2013, 2012; Hinkelman and Loeb, 2007; Vanderwel et al., 2010).

Habitat associations of small mammals are most frequently assessed using abundance estimates or indices thereof (e.g., Converse et al., 2006; Coppeto et al., 2006; Fauteux et al., 2012). Several studies, however, have argued that abundance alone is not necessarily a good proxy for habitat quality (e.g., Battin, 2004; Robertson and Hutto, 2006; Van Horne, 1983). Areas with high abundance can consist of suboptimal or even sink habitats, harboring the “spillover” from high quality, or source habitat. Often, these sinks harbor competitively inferior individuals that are unable to establish themselves in high quality patches (Ecke et al., 2002; Van Horne, 1983). To disentangle the effects of habitat quality and competition, it is important to look at abundance in combination with indicators of physical condition of animals, such as their body mass (Greenberg et al., 2006).

Live trapping is a standard tool in the study of small mammal populations. Although the importance of accounting for imperfect and varying detection probability in the study of animal populations has long been recognized (e.g., Nichols, 1992; Otis et al., 1978), many contemporary small mammal studies still ignore detection bias and draw inference on raw counts (e.g., Amacher et al., 2008; Bellows et al., 2001; Coppeto et al., 2006; Fauteux et al., 2012; Kelt et al., 2013; Lee et al., 2008). When combined with capture-recapture modeling, however, live trapping studies can produce unbiased estimates of abundance while accounting for imperfect detection probability (e.g., Converse et al., 2006; Monroe and Converse, 2006). If applied at various sites, estimates can be related to site-level covariates. Until recently, such analyses have mostly been applied post hoc (Converse et al., 2006), or directly to uncorrected numbers of individuals captured (see above). The latter approach fails to account for detection probability, and thus carries an inherent risk of bias, especially when detection varies by species or with covariates that are considered to influence abundance (e.g., Monroe and Converse, 2006). Post hoc regression of abundance estimates against predictor variables is complicated because uncertainty of the estimates, which is bound to vary in its magnitude across estimates, has to be taken into account (Converse et al., 2006). Recent model developments allow for the joint estimation of abundance and its response to covariates across multiple sites (or otherwise defined groups) in a unified capture-recapture framework for stratified populations (Converse and Royle, 2012; Royle et al., 2014). The approach accounts for imperfect detection,

and allows modeling of population level response to explanatory covariates, while fully accounting for uncertainty on all levels of the model. Although this conceptually coherent analytical framework accommodates a data structure that is common in the study of small mammals, it remains infrequently used.

Here, we use capture-recapture (CR) models for stratified populations to investigate the response of the small mammal community to habitat features that have been altered by recent forestry practices. Our study spans three years of live trapping data collected across 23 sites in the Lake Tahoe Basin of the Sierra Nevada, which was heavily logged during the mid-19th century. We investigate how forest structure impacts the abundance and physical condition of 8 small mammal species associated with these traditionally frequent-disturbance forests. Based on the available literature, we predict that higher levels of coarse woody debris and lower levels of canopy cover will positively affect small mammal abundance and physical condition. The results of this study contribute to our understanding of how small mammal communities that evolved under a frequent fire regime are shaped by forest structure and by competition.

Material and methods

Study site

We used live-trapping data from 23 sites in the upland forests of the Lake Tahoe Basin, straddling the states of California and Nevada, USA, in the central Sierra Nevada. The basin lies in a transition zone between Mediterranean and continental climates, creating a great diversity of habitats and leading to the juxtaposition of habitat for several small mammal species. Prior to Euro-American influence, the basin experienced fires every 3–4 years with site fire return intervals of every 8–17 years. A century of fire suppression, intensive logging, and urbanization has resulted in homogenization of the basin's landscapes and coarse scale heterogeneity (Beatty and Taylor, 2008). Our study sites were located in the lower montane zone at altitudes of 1900–2250 m, and dominated by Jeffrey pine (*Pinus jeffreyi*) forest, white fir (*Abies concolor*) forest, and mixed-conifer forest (Jeffrey pine, white fir, incense cedar *Calocedrus decurrens*, sugar pine *P. lambertiana*, and red fir *A. magnifica*).

Small mammal trapping

At each site, we established one trapping grid that was sampled in two of three consecutive years (13 sites in 2009/2010, 10 sites 2010/2011), resulting in 46 site-year combinations, which constitute the sampling groups. Each trapping grid consisted of 72 (2009), 54 (2010) and 48 (2011) trap stations (reduced over time due to logistical constraints) with a 30-m spacing between stations. This design represents a balance between covering a sufficient number of home ranges of the larger squirrels and obtaining a high enough recapture rate for the smaller species to obtain reliable estimates of density (Converse et al., 2006). At each station we set one Tomahawk trap (12 × 12 × 40 cm) and one extra-large Sherman trap (10 × 11 × 38 cm). Tomahawk traps were attached to trees >20 in diameter at breast height, 1.5–2.0 m above ground, and wrapped in a polytarp for cover. Sherman traps were placed at the base of trees, along larger logs or under shrubs, covered with natural materials to insulate them from sun and rain, and with polystyrene in the back to provide further insulation. We baited all traps with a mixture of oats, peanut butter, raisins, and molasses. We pre-baited traps for 3–4 days and subsequently opened traps for a single 4.5-day trapping period, checking traps in the morning and evening. With the exception of shrews, all individuals were marked with uniquely numbered ear tags (model 1005-1). We recorded the species, age,

sex and body mass of all captured animals. Month of trapping varied among sites and occurred in either June, July or August when hibernating species are active above ground.

Site-level covariates

For each site, canopy cover and coarse woody debris were measured at 8–10 randomly selected points on the trapping grid in either 2010 or 2011. Any changes occurring in these variables across the three years would have been minimal, so a single measurement was adequate to characterize habitat structure. Canopy cover was estimated using 25 densitometer readings taken in a 5×5 configuration with 5-m spacing placed at the center of the trapping grid. Coarse woody debris was sampled along four 17.6-m transects in each grid using the line-intercept method (Brown and Johnston 1976). Transects ran in each cardinal direction from the grid's center. Volume of CWD was based on material with ≥ 7.5 cm diameter and estimated following Waddell (2002).

Data analysis

Effects of habitat on abundance

For 8 species there was a sufficient number of individuals (>100 across all groups) captured for analysis (Table 1). We investigated the relationship between species abundance and habitat using capture-recapture (CR) models for stratified populations. In short, these models use standard CR encounter histories from repeated sampling occasions to estimate abundance at multiple sites or otherwise defined groups; and link these estimates with a model describing how abundance varies across groups as a function of covariates. This hierarchical model presents a coherent framework for such data to investigate drivers of small mammal populations in a statistically robust manner. Following Converse and Royle (2012), we assume that the (unknown) group-specific population sizes, N_g , follow a Poisson distribution with mean λ_g . Group-level covariates on λ_g can then be modeled on the log-scale as in standard Poisson regression. Specifically, we included two site-level habitat variables, volume of coarse woody debris (CWD) and percent canopy cover (PCC), both of which have been shown to influence habitat quality for many small mammal species (Hallett et al., 2003). We further included a year effect to account for fluctuations in small mammal populations across years, which are generally pronounced (Hallett et al., 2003). Thus, our model for group-level abundance (i.e., abundance for each site/year combination) takes the form:

$$N_g \sim \text{Poisson}(\lambda_g)$$

$$\log(\lambda_g) = \beta_0 + \beta_1 \text{CWD}_g + \beta_2 \text{PCC}_g + \beta_3 Y10_g + \beta_4 Y11_g$$

Here, β_0 is the intercept in year 2009, and $Y10$ and $Y11$ are “dummy variables”, taking on the value of 1 if group g was surveyed in 2010 ($Y10$) or 2011 ($Y11$), and 0 if not.

Group-level abundance, N , is unknown, but can be estimated from individual-level detection data. Royle et al. (2014) noted that the above model for variation in group abundance can be expressed as an individual-level CR model by introducing an individual covariate describing group membership, g_i . Possible values of g_i are 1, 2, ..., G , for G groups, and for the Poisson abundance model described above, g_i has a multinomial distribution with cell probabilities π defined by:

$$\pi_g = \frac{\lambda_g}{\sum_G \lambda_g}$$

To estimate the total number of individuals across all groups – the superpopulation – N_S , we employ data augmentation (Royle and Dorazio, 2012). We let n_S be the total number of individuals

observed across all G groups. We augment the observed data set with a large number, $M - n_S$, of all-zero encounter histories representing hypothetical individuals, and estimate which of these individuals are part of the superpopulation. Here, M is an arbitrary value chosen large enough so that estimates of N_S are not truncated by the choice of M . To fit this model, we introduce a binary individual variable, z_i , which is 1 if the individual is part of N_S and 0 otherwise:

$$z_i \sim \text{Bernoulli}(\Psi)$$

N_S can then be derived as the sum of all z_i , and estimates of N_g can be obtained by summing over all individuals for a given group with $z_i = 1$. Both z_i and g_i are latent for augmented individuals.

The observation model is a standard capture-recapture model, in which the detection of individual i at sampling occasion k , y_{ik} (1 if detected, 0 if not detected), is assumed to be a Bernoulli random variable with capture probability p_{ik} :

$$y_{ik} \sim \text{Bernoulli}(p_{ik}).$$

We model variation in p_{ik} on the logit scale. On the individual level, we included a behavioral response to previous capture, denoted by C_{ik} , which is 1 if the individual has been captured in a previous occasion, and 0 otherwise. On the group level, we included a random site-specific intercept to account for variability in detection induced by unmeasured local factors, α_S ; and an effect of the month of trapping ($M07$ and $M08$ for July and August, respectively, with the intercept referring to the month of June), because some of the investigated species spend different amounts of time above ground, thus being more or less available to trapping, depending on time of the year and climatic conditions (e.g., Feldhamer et al., 1993; Maguire, 1999):

$$\text{logit}(p_{ik}) = \alpha_{S[g_i]} + \alpha_1 C_{ik} + \alpha_2 M07 + \alpha_3 M08$$

$$\alpha_{S[g_i]} \sim \text{Normal}(\mu_\alpha, \sigma_\alpha^2)$$

Hyperparameters of the random effects distribution, μ_σ and σ_α , are estimated as part of the model using noninformative uniform priors. In the present study we had one capture history for Sherman and one for Tomahawk traps. We used the above described detection model for the Sherman encounter data. We used the same intercept and predictors in the Tomahawk detections model, but added an effect of trap type, and constructed a separate behavioral response (C) matrix for Tomahawk traps, assuming that small mammals previously caught in a Sherman trap would not automatically exhibit trap response to Tomahawk traps, but that trap response overall would be the same for both traps types.

For northern flying squirrels, deer mice, and California ground squirrels data were insufficient to implement this fully parameterized model, so we replaced the random intercept in detection with a constant intercept. Only one deer mouse was ever captured in a Tomahawk trap. We excluded this capture from the data and removed the effect of trap type from the model.

We implemented the models in JAGS (Plummer, 2003), accessed through R version 2.15.2 (R Core Team, 2014), running 3 parallel chains with 30,000 iterations following a burn-in phase of 500 iterations. We used the Gelman-Rubin statistic to assess chain convergence (Gelman et al., 2004). Values below 1.1 indicate parallel chains have converged to the same stationary distribution; for all parameters in all models, the statistic was <1.1 . We report results as the posterior mean with standard deviation. We consider an effect of a covariate to be strong if the Bayesian Credible Interval of the coefficient (BCI; defined as the 2.5% and 97.5% quantiles of the posterior distribution) does not overlap 0.

Table 1
Small mammal species, total number of individuals captured, total captures and number of individuals recaptured on 23 live-trapping grids surveyed twice between 2009 and 2011 from the Sierra Nevada, California.

Common name	Latin name	Abbreviation	Individuals captured	Total captures	Individuals recaptured
Golden-mantled ground squirrel	<i>Callospermophilus lateralis</i>	CALA	309	691	175
Northern flying squirrel	<i>Glaucomys sabrinus</i>	GLSA	134	200	41
California ground squirrel	<i>Otospermophilus beecheyi</i>	OTBE	236	662	157
Deer mouse	<i>Peromyscus maniculatus</i>	PEMA	642	781	87
Yellow-pine chipmunk	<i>Tamias amoenus</i>	TAAM	1198	3174	768
Long-eared chipmunk	<i>Tamias quadrimaculatus</i>	TAQU	1132	3069	751
Allen's chipmunk	<i>Tamias senex</i>	TASE	393	1267	270
Lodgepole chipmunk	<i>Tamias speciosus</i>	TASP	214	665	152

Spatial versus non-spatial hierarchical CR models

This model formulation is equally amenable to traditional or spatial capture-recapture (SCR) models (Royle and Converse, 2014). Spatial capture-recapture models have several advantages over traditional capture-recapture: they account for differential exposure to trapping due to individual location relative to the trapping grid, and they provide a coherent framework for the estimation of density. While the conceptual development of such a model is straight forward, the resulting model for our data set proved too slow and memory-intensive to be feasible. To validate use of non-spatial CR models, we compared abundance estimates for a subset of groups from single-group SCR models and our non-spatial model. Results of these analyses are shown in Appendix A.

Effect of habitat on body mass

Abundance alone can provide misleading information about habitat quality for a species (e.g., Van Horne, 1983). Therefore, we also investigated the effect of forest structure on average body mass of the sampled small mammal groups. We used a linear mixed model to fit individual body mass as a function of CWD and PCC, controlling for possible year effects (Y10 and Y11). We only considered adults in this analysis, which constituted the vast majority of captured individuals and were distinguished from non-adults based on size and reproductive maturity. To account for different variances in body mass (*mass*) among groups we included a group-specific random standard deviation, σ_g , having an inverse-gamma distribution:

$$mass_i \sim \text{Normal}(\mu_{g[i]}, \sigma_{g[i]}^2)$$

$$\mu_{g[i]} = \alpha W_g + \beta_1 PCC + \beta_2 CWD + \beta_3 Y10 + \beta_4 Y11$$

$$\frac{1}{\sigma_{g[i]}^2} \sim \text{Gamma}(r, q)$$

For some species, hyperparameters of the random effects distributions (r and q) were not estimable; in these cases we restricted the model to a single shared σ_g^2 parameter with a uniform prior. The model allows us to predict average body mass in groups without any captured individuals based on the estimated regression coefficients.

We implemented the model in JAGS, accessed through R, running 3 parallel Markov chains with a 500-iteration burn-in and 20,000 post burn-in iterations, thinning by 10. We assessed convergence and report results as described in the previous section.

Total abundance and biomass

The CR model accounted for variation in abundance across groups for each species, but we were also interested in broader trends in the response of the small mammal community to habitat covariates. Therefore, for each group we summed estimates of abundance for all species to obtain an estimate of total small mammal abundance. Based on the total abundance of all species

within each group and the group-mean body mass, we calculate the total small mammal biomass per group. Because parameter estimates are associated with varying degrees of uncertainty, performing statistical tests on estimates is not desirable. Therefore, we plotted total abundance and total biomass against the two habitat covariates (CWD and PCC) and visually assessed trends.

Results

Covariate effects on species abundance and detection

Percent canopy cover (PCC) ranged from 27 to 59.5%, and coarse woody debris (CWD) ranged from 100.76 to 2487.86 m³/ha, with all but one site <720 m³/ha.

Abundances of species responded differently to habitat variables (Table 2; estimates of abundance for all groups and species can be found in Appendix B). PCC had a strong negative relationship with abundance for yellow-pine chipmunks and California ground squirrels, and a strong positive relationship for deer mice. The volume of CWD had a strong negative effect on the abundance of golden-mantled ground squirrels, yellow-pine and long-eared chipmunks, and a strong positive effect on deer mice. Yearly fluctuations in abundance, expressed as changes in abundance relative to 2009, were significant for at least one year (2010 or 2011) for all species but Allen's chipmunk.

Capture probabilities increased strongly after first capture for all species but the northern flying squirrel (weak positive effect) and the deer mouse (strong negative effect; Table 2). Long-eared and Allen's chipmunks had similar capture probabilities across the two trap types, while capture probabilities differed between trap types for all other species. Only the golden-mantled ground squirrel and Allen's chipmunk did not show differences in capture probabilities among months of trapping.

Effect of habitat on body mass

We were able to estimate a group-specific standard deviation of body mass for deer mice, golden-mantled ground squirrels, and yellow-pine, long-eared and Allen's chipmunks, thereby accounting for differences in within-group body mass variation (Appendix B). CWD had a strong positive association and PCC had a strong negative association with body mass for deer mice, golden-mantled ground squirrels and yellow-pine chipmunks (Table 3). In addition, most species, with the exception of golden-mantled and northern flying squirrels, exhibited a strong positive year effect on body mass for at least one of the years (2009 or 2010).

Total abundance and biomass

Total small mammal abundance per group ranged from 70.62 to 321.47 individuals, and total biomass ranged from 3862 to 37,945 g (Appendix B). The plots of total abundance and total biomass

Table 2

Covariate effects (with standard deviation) on abundance and detection (on log and logit scale, respectively) from a capture-recapture model for stratified populations for 8 small mammal species live-trapped in the Sierra Nevada between 2009 and 2011.

	Abundance covariates				Detection covariates			
	PCC	CWD	2010	2011	Recapture	Tomahawk	July	Aug
CALA	−0.06 (0.07)	−1.03 ^a (0.20)	−1.04 ^a (0.20)	−2.21 ^a (0.22)	0.76 ^a (0.07)	−2.06 ^a (0.14)	0.07 (0.17)	0.14 (0.23)
GLSA ^b	−0.02 (0.08)	0.01 (0.07)	1.10 ^a (0.24)	−0.51 (0.36)	0.18 (0.27)	1.67 ^a (0.20)	−0.30 (0.21)	−0.79 ^a (0.27)
OTBE ^b	−0.37 ^a (0.08)	−0.09 (0.10)	1.33 ^a (0.18)	0.10 (0.25)	1.07 ^a (0.12)	−0.48 ^a (0.09)	0.61 ^a (0.17)	0.46 ^a (0.22)
PEMA ^b	0.10 ^a (0.04)	0.13 ^a (0.03)	−1.57 ^a (0.09)	−3.45 ^a (0.31)	−1.11 ^a (0.16)	NA	0.44 ^a (0.15)	0.33 ^a (0.15)
TAAM	−0.18 ^a (0.04)	−1.50 ^a (0.14)	0.05 (0.08)	−0.36 ^a (0.10)	0.68 ^a (0.05)	−1.05 ^a (0.05)	0.14 ^a (0.06)	−0.18 (0.09)
TAQU	−0.06 (0.04)	−0.26 ^a (0.05)	0.48 ^a (0.08)	0.06 (0.12)	0.36 ^a (0.04)	0.06 (0.04)	0.45 ^a (0.08)	0.25 ^a (0.11)
TASE	0.06 (0.07)	−0.08 (0.06)	−0.07 (0.14)	0.20 (0.18)	0.67 ^a (0.08)	0.06 (0.06)	0.04 (0.12)	0.26 (0.16)
TASP	0.06 (0.11)	0.02 (0.07)	1.13 ^a (0.26)	−0.06 (0.29)	0.57 ^a (0.10)	−0.46 ^a (0.09)	−0.24 ^a (0.12)	−0.06 (0.23)

2010/2011: difference in abundance relative to year 2009. July/Aug: difference in detection relative to June. Tomahawk: difference in detection relative to Sherman trap. Recapture: effect on detection of an animal having been captured before.

^a 95% BCI does not include 0; strong effect.

^b Detection model does not include a random site-specific intercept.

Table 3

Estimates of covariate effects (with posterior standard deviation) on group-mean body mass from the generalized linear mixed model for 8 small mammal species live-trapped in the Sierra Nevada between 2009 and 2011.

	PCC	CWD	2010	2011
CALA ^b	−0.48 (0.13) ^a	1.10 (0.54) ^a	4.99 (3.05)	−3.30 (4.18)
GLSA	−0.31 (0.23)	0.35 (0.45)	−3.29 (3.97)	3.03 (6.17)
OTBE	−0.45 (1.58)	0.20 (6.80)	90.05 (23.26) ^a	83.14 (29.11) ^a
PEMA ^b	−0.04 (0.02) ^a	0.08 (0.02) ^a	−0.02 (0.37)	3.28 (1.59) ^a
TAAM ^b	−0.13 (0.01) ^a	0.25 (0.09) ^a	0.25 (0.40)	1.74 (0.50) ^a
TAQU ^b	−0.16 (0.03)	0.08 (0.12)	1.88 (0.72) ^a	2.22 (0.98) ^a
TASE ^b	0.06 (0.07)	0.15 (0.10)	4.09 (1.22) ^a	−0.79 (2.01)
TASP	0.04 (0.10)	−0.38 (0.45)	0.59 (1.52)	4.42 (1.87) ^a

^a 95% BCI does not include 0; strong effect.

^b Model includes a random group-specific standard deviation.

against PCC and CWD showed negative trends; trends appeared to be stronger for CWD than for PCC (Fig. 1).

Discussion

Worldwide, many forests that were actively managed for timber production in the 19th and 20th centuries are comprised of younger and less structurally diverse stands – changes that can ultimately impact the habitat resources for forest-dwelling species (Carey and Johnson 1995). In boreal and more mesic forests of the western United States, the loss of old-growth forest has raised concerns regarding the sustainability of species that specialize on old-growth habitat (Kelt et al., 2013; Smith, 2007; USDA, 2004). However, populations of species that occupy forests that historically experienced more frequent disturbances may not be subject to the same ecological constraints as populations that inhabit more stable environments.

In the frequent-fire forests of the Lake Tahoe Basin, several small mammal species share the same ecosystem at considerable abundances. The most abundant species in the present study varied across sites, and, at most sites, changed between years (Appendix B), suggesting that individual species in frequent disturbance forests are adaptable to a variety of forest conditions. Indeed, even the northern flying squirrel, which is frequently associated with closed-canopy, old-growth forests (Carey and Johnson, 1995; Smith et al., 2005), was found at the majority of our sites, and not found to be positively associated with canopy cover (see also Smith, 2007). Although theory generally predicts coexistence through specialization (Schoener, 1974), coexistence of species with broad niche overlap has frequently been recorded (e.g., De León et al., 2014; Martin and Genner, 2009). Our focus on habitat only captures one primary axis of a species' niche, and it is conceivable that the species in the present study are habitat generalists with divergent dietary or temporal niches.

Concurrent with our expectations, forest stands with a more closed canopy harbored small mammals at lower abundance and biomass (Fig. 1). Increasing canopy cover may limit resources important to small mammals by reducing understory structure. This is corroborated by a strong negative association between canopy cover and shrub cover across our study sites (data not shown; see also Knapp et al., 2013). Establishment of an individual in an area with lower resource availability could impact individual body mass and ultimately individual survival and reproductive output (Lindström, 1999), leading to lower abundances and body condition of small mammals under more closed canopy conditions. Deer mice were the only species in our study to be positively associated with canopy cover. As the smallest of all investigated species, deer mouse populations may be influenced more strongly by local abundances of the larger competitors, thriving where the larger species are less common.

While the relationships of small mammals with canopy cover were consistent with previous studies, the effects of coarse woody debris were less clear. Previous studies have stressed the importance of coarse woody debris as a habitat feature for ground-dwelling small mammals (Carey and Johnson, 1995; Ecke et al., 2002; Fauteux et al., 2013, 2012; Hinkelman et al., 2012; Vanderwel et al., 2010). In the present study, the volume of CWD was positively associated with mean body mass and negatively associated with abundance in some species, and seemed to have a negative association with overall abundance and biomass. CWD provides microclimate suitable for lichen, fungi and insects, important food resources for the small mammals investigated here (Luoma et al., 2003). Thus, higher volumes of CWD should be associated with higher quality and/or abundance of food resources, explaining its positive link to body mass. It is conceivable that we see a pattern in some species (golden-mantled ground squirrel, yellow-pine chipmunk), where heavier, more competitive individuals monopolize high-quality sites by driving out less competitive individuals, thus

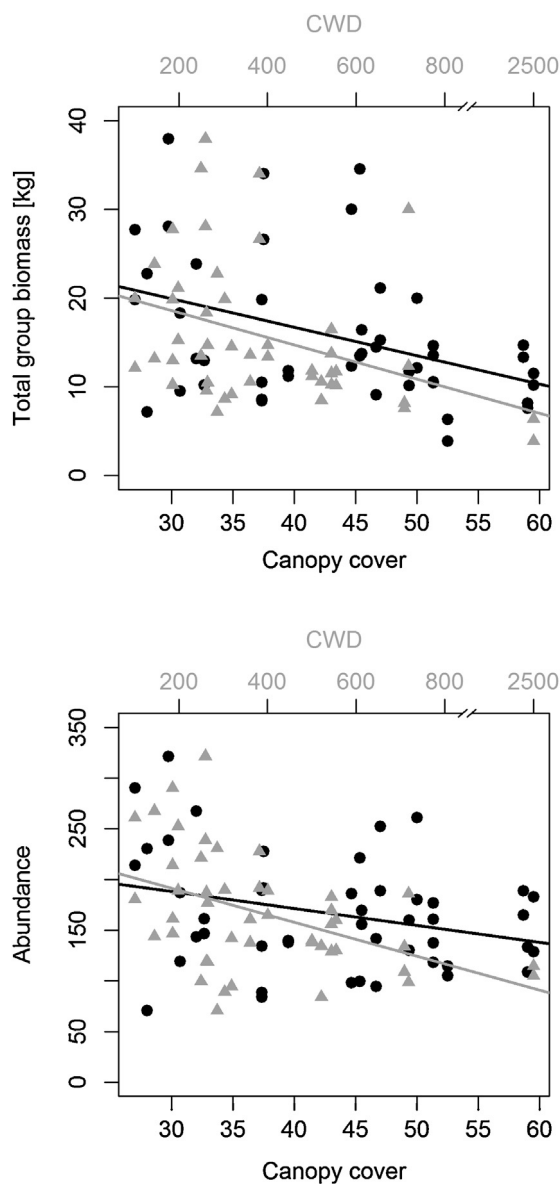


Fig. 1. Total small mammal abundance (bottom) and biomass (top) per group plotted against canopy cover (black circles) and coarse woody debris (grey triangles), with linear trend lines.

limiting site abundance (Ecke et al., 2002). We did not, however, see analogous patterns in the relationships between abundance, body mass and canopy cover. Alternatively, individuals of mean higher body mass at lower abundances can result when an area provides the necessary food resources, but individuals occupying the area have lower survival. For instance, predation is known to affect survival and abundance of small mammals (e.g., Fitzgerald, 1977), but might not affect body condition (Predator-pit hypothesis, Haber, 1977). Hinkelman et al. (2012), for example, found that CWD increased the perceived risk of predation for small mammals foraging on the ground and attributed this to the abundance of rodent-eating snakes. This combination of factors could lead to a habitat with abundant food resources and high predator-caused mortality, thus limiting overall abundance.

Although the average volume of CWD in this study was comparable to other, ecologically similar sites, the average size of logs was lower than in other areas of the Sierra Nevada (Lydersen and North, 2012; Stephens et al., 2007). Early stand development in a previously logged area can result in larger quantities of small diameter

CWD that, without fire, remain in the system for longer periods of time. These changes to the structure of CWD can alter its utility to small mammals. For instance, small mammals frequently use logs to facilitate movement and possibly to reduce auditory detection by predators (Roche et al., 1999). When CWD is smaller, these “free-ways” become “country roads”, possibly increasing travel costs and susceptibility to predation. The change in the structure of CWD resulting from over 100 years of fire suppression (Knapp 2015) may have ultimately altered its function resulting in an ecological trap for small mammals (Battin, 2004; Robertson and Hutto, 2006). Thus, the mere volume of CWD might not be a good descriptor of how small mammals use CWD, and might be insufficient when studying habitat associations of these species.

Year effects were present in more species and often stronger than habitat effects, for both body mass and abundance (Tables 2 and 3). Variations in population size between years are typical of small mammals (Hallett et al., 2003; Monroe and Converse, 2006) and complicate identifying other factors affecting abundance, especially in short-term studies. Year effects can represent stochastic fluctuations, or deterministic effects, for example of climate (e.g., Bagne and Finch, 2010) or high resource abundance. In our study, year effects on abundance were variable across species, suggesting that annual conditions did not impact small mammal communities uniformly, or that stochasticity plays a predominant role in the observed fluctuations. Examining 2011, however, all strong effects on abundance were negative (Table 2). The winter preceding the 2011 field season was an extremely heavy snow year, which may have reduced small mammal populations. Year effects on body mass in both years were consistently positive when significant, again suggesting that different factors regulate body mass and abundance.

Methodological considerations

CR models for stratified populations are a powerful tool for inference in spatially and temporally sampled populations, which often occurs in small mammal studies. They are particularly useful when modeling data sets that by themselves (at the group-level) might be too sparse to be analyzed, because they allow information to be ‘borrowed’ across groups. The use of non-spatial capture-recapture models has lately fallen into disfavor in many applications, due to the development of improved, spatial capture-recapture (SCR) models. We were unable to implement a stratified-population SCR model because it was too memory and time consuming. Results of our analysis of a subset of the data with single-group SCR models showed that abundance estimates from the non-spatial model were positively correlated with the spatial model estimates of abundance (Appendix A). Further, for most species movement varied among grids but was narrow relative to grid size. Thus, our non-spatial models seem to allow reliable inference on spatial variation in abundance in this particular case. Due to the general shortcomings of non-spatial CR models and because the similarities observed here may not always present in other studies, we advocate the use of SCR models whenever possible.

Conclusion

Concerns about fuel load and ambitions to restore fire cycles in western forest ecosystems have sparked a large number of studies investigating the effects of thinning on habitat structure, and, consequently, on small mammals and other species communities. In particular, CWD is generally thought to be positively associated with the abundance of small mammals. Conversely, we found that increasing amounts of CWD supported less small mammal biomass, while more open forests sustained more individuals in better

physical condition. This points to a need to investigate the link between physical structure and ecological function of CWD. Higher abundances of small mammals in more open forests is in agreement with the hypothesis that small mammals in the Lake Tahoe region evolved under a frequent disturbance regime, and are therefore not expected to be closed-forest specialists. Alternatively, it has been proposed that the absence of closed forest specialist species, and the prevalence of a generalist small mammal community, is the result of structural homogenization of the Sierra Nevada forests (Kelt et al. 2013). Both hypotheses suggest that the contemporary forests predominantly consisting of dense even-aged stands may negatively impact the small mammal community.

Acknowledgements

This work was made possible by the hard work of our field crews, particularly Scott Appleby, Katrina Heckendorn and Amy Sturgill. Eric Newkirk and Tray Biasioli assisted with database management. We thank the managers in the Lake Tahoe Basin Management Unit for their continued support. We further thank J. Andrew Royle and Sarah Converse for advice on stratified CR models, RENCI for access to a high performance computer when we explored spatial CR analysis of the data, and Takashi Saitoh and three anonymous reviewer for valuable comments on an earlier draft of this manuscript. Funding was provided by US Forest Service Pacific Southwest Research Station, and the Sierra Nevada Public Lands Management Act. Any use of trade, product, or firm names is for descriptive purposes only and does not imply endorsement by the US Government.

Appendix A. Supplementary data

Supplementary material related to this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.mambio.2015.03.002>

References

- Amacher, A.J., Barrett, R.H., Moghaddas, J.J., Stephens, S.L., 2008. Preliminary effects of fire and mechanical fuel treatments on the abundance of small mammals in the mixed-conifer forest of the Sierra Nevada. *Forest Ecol. Manag.* 255, 3193–3202.
- Bagne, K.E., Finch, D.M., 2010. Response of small mammal populations to fuel treatment and precipitation in a ponderosa pine forest, New Mexico. *Restoration Ecol.* 18, 409–417.
- Battin, J., 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conserv. Biol.* 18, 1482–1491.
- Beatty, R.M., Taylor, A.H., 2008. Fire history and the structure and dynamics of a mixed conifer forest landscape in the northern Sierra Nevada, Lake Tahoe Basin, California, USA. *Forest Ecol. Manag.* 255, 707–719.
- Bellows, A.S., Pagels, J.F., Mitchell, J.C., 2001. Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia. *Am. Midl. Nat.* 146, 345–360.
- Brown, J.K., Johnston, C.M., 1976. Debris Prediction System. Intermountain Forest and Range Experiment Station.
- Carey, A.B., Johnson, M.L., 1995. Small mammals in managed, naturally young, and old-growth forests. *Ecol. Appl.* 5, 336–352.
- Carey, A.B., Kershner, J., Biswell, B., de Toledo, L.D., 1999. Ecological scale and forest development: squirrels, dietary fungi, and vascular plants in managed and unmanaged forests. *Wildlife Monogr.* 142, 3–71.
- Converse, S.J., Royle, J.A., 2012. Dealing with incomplete and variable detectability in multi-year, multi-site monitoring of ecological populations. In: Gitzen, R.R., Millsbaugh, J.J., Cooper, A.B., Licht, D.S. (Eds.), *Design and Analysis of Long-Term Ecological Monitoring Studies*. Cambridge University Press, pp. 426–442.
- Converse, S.J., White, G.C., Farris, K.L., Zack, S., 2006. Small mammals and forest fuel reduction: national-scale responses to fire and fire surrogates. *Ecol. Appl.* 16, 1717–1729.
- Coppeto, S.A., Kelt, D.A., Van Vuren, D.H., Wilson, J.A., Bigelow, S., 2006. Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. *J. Mammal.* 87, 402–413.
- De León, L.F., Podos, J., Gardezi, T., Herrel, A., Hendry, A.P., 2014. Darwin's finches and their diet niches: the sympatric coexistence of imperfect generalists. *J. Evol. Biol.* 27, 1093–1104.
- Devictor, V., Julliard, R., Jiguet, F., 2008. Distribution of specialist and generalist species along spatial gradients of habitat disturbance and fragmentation. *Oikos* 117, 507–514.
- Ecke, F., Löfgren, O., Sörilin, D., 2002. Population dynamics of small mammals in relation to forest age and structural habitat factors in northern Sweden. *J. Appl. Ecol.* 39, 781–792.
- Fauteux, D., Imbeau, L., Drapeau, P., Mazerolle, M.J., 2012. Small mammal responses to coarse woody debris distribution at different spatial scales in managed and unmanaged boreal forests. *Forest Ecol. Manag.* 266, 194–205.
- Fauteux, D., Mazerolle, M.J., Imbeau, L., Drapeau, P., 2013. Site occupancy and spatial co-occurrence of boreal small mammals are favoured by late-decay woody debris. *Can. J. Forest Res.* 43, 419–427.
- Feldhamer, G.A., Klann, R.S., Gerard, A.S., Driskell, A.C., 1993. Habitat partitioning, body size, and timing of parturition in pygmy shrews and associated soricids. *J. Mammal.* 74, 403–411.
- Fitzgerald, B.M., 1977. Weasel predation on a cyclic population of the montane vole (*Microtus montanus*) in California. *J. Anim. Ecol.* 46, 367–397.
- Gelman, A., Carlin, J.B., Stern, H.S., Rubin, D.B., 2004. *Bayesian Data Analysis*, second edition. CRC/Chapman & Hall, Boca Raton, Florida, USA.
- Greenberg, C.H., Otis, D.L., Waldrop, T.A., 2006. Response of white-footed mice (*Peromyscus leucopus*) to fire and fire surrogate fuel reduction treatments in a southern Appalachian hardwood forest. *Forest Ecol. Manag.* 234, 355–362.
- Haber, G.C. (Ph.D.) 1977. Socio-ecological dynamics of wolves and prey in a subarctic ecosystem. University of British Columbia, Vancouver, Canada.
- Hallett, J.G., O'Connell, M.A., Maguire, C.C., 2003. Ecological relationships of terrestrial small mammals. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, New York, pp. 120–156.
- Hinkelman, T.M., Loeb, S.C., 2007. Effect of woody debris abundance on daytime refuge use by cotton mice. *Southeast. Nat.* 6, 393–406.
- Hinkelman, T.M., Orrock, J.L., Loeb, S.C., 2012. Effect of downed woody debris on small mammal anti-predator behavior. *Ethology* 118, 17–23.
- Johnston, A.N., Anthony, R.G., 2008. Small-mammal microhabitat associations and response to grazing in Oregon. *J. Wildl. Manag.* 72, 1736–1746.
- Kassen, R., 2002. The experimental evolution of specialists, generalists, and the maintenance of diversity. *J. Evol. Biol.* 15, 173–190.
- Kelt, D.A., Van Vuren, D.H., Johnson, M.L., Wilson, J.A., Innes, R.J., Jesmer, B.R., Ingram, K.P., Smith, J.R., Bigelow, S.W., Burnett, R.D., Stine, P.A., 2013. Small mammals exhibit limited spatiotemporal structure in Sierra Nevada forests. *J. Mammal.* 94, 1197–1213.
- Knapp, E.E., 2015. Long-term dead wood changes in a Sierra Nevada mixed conifer forest: habitat and fire hazard implications. *Forest Ecol. Manag.* 339, 87–95.
- Knapp, E.E., Skinner, C.N., North, M.P., Estes, B.L., 2013. Long-term overstory and understorey change following logging and fire exclusion in a Sierra Nevada mixed-conifer forest. *Forest Ecol. Manag.* 310, 903–914.
- Lawlor, T.E., 2003. Faunal composition and distribution of mammals in western coniferous forests. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, New York, pp. 41–80.
- Lee, E.-J., Lee, W.-S., Rhim, S.-J., 2008. Characteristics of small rodent populations in post-fire silvicultural management stands within pine forest. *Forest Ecol. Manag.* 255, 1418–1422.
- Lemaître, J., Fortin, D., Morris, D.W., Darveau, M., 2010. Deer mice mediate red-backed vole behaviour and abundance along a gradient of habitat alteration. *Evol. Ecol. Res.* 12, 203–216.
- Lindström, J., 1999. Early development and fitness in birds and mammals. *Trends Ecol. Evol.* 14, 343–348.
- Luoma, D.L., Trappe, J.M., Claridge, A.W., Jacobs, K.M., Cazares, E., 2003. Relationships among fungi and small mammals in forested ecosystems. In: Zabel, C.J., Anthony, R.G. (Eds.), *Mammal Community Dynamics: Management and Conservation in the Coniferous Forests of Western North America*. Cambridge University Press, New York, pp. 343–373.
- Lydersen, J., North, M., 2012. Topographic variation in structure of mixed-conifer forests under an active-fire regime. *Ecosystems* 15, 1134–1146.
- Maguire, C.C., 1999. Rainfall, ambient temperature, and *Clethrionomys californicus* capture frequency. *Mammal Rev.* 29, 135–142.
- Martin, C.H., Genner, M.J., 2009. High niche overlap between two successfully coexisting pairs of Lake Malawi cichlid fishes. *Can. J. Fish. Aquat. Sci.* 66, 579–588.
- Monroe, M.E., Converse, S.J., 2006. The effects of early season and late season prescribed fires on small mammals in a Sierra Nevada mixed conifer forest. *Forest Ecol. Manag.* 236, 229–240.
- Naxara, L., Pinotti, B.T., Pardini, R., 2009. Seasonal microhabitat selection by terrestrial rodents in an old-growth Atlantic Forest. *J. Mammal.* 90, 404–415.
- Nichols, J.D., 1992. Capture-recapture models. *Bioscience* 42, 94–102.
- Otis, D.L., Burnham, K.P., White, G.C., Anderson, D.R., 1978. Statistical inference from capture data on closed animal populations. *Wildlife Monogr.* 62, 1–135.
- Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: *Proceedings of the 3rd International Workshop on Distributed Statistical Computing*, pp. 20–22.
- Price, M.V., Jenkins, S.H., 1987. Rodents as seed consumers and dispersers. In: Murray, D.R. (Ed.), *Seed Dispersal*. Academic Press, Sydney, NSW, Australia, pp. 191–235.
- Pyare, S., Longland, W.S., 2001. Patterns of ectomycorrhizal-fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. *J. Mammal.* 82, 681–689.

- R Core Team, 2014. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Robertson, B.A., Hutto, R.L., 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87, 1075–1085.
- Roche, B.E., Schulte-Hostedde, A.I., Brooks, R.J., 1999. Route choice by deer mice (*Peromyscus maniculatus*): reducing the risk of auditory detection by predators. *Am. Midl. Nat.* 142, 194–197.
- Royle, J.A., Chandler, R.B., Sollmann, R., Gardner, B., 2014. *Spatial Capture–Recapture*. Academic Press, Waltham, MD, USA.
- Royle, J.A., Converse, S.J., 2014. Hierarchical spatial capture–recapture models: modelling population density in stratified populations. *Methods Ecol. Evol.* 5, 37–43.
- Royle, J.A., Dorazio, R.M., 2012. Parameter-expanded data augmentation for Bayesian analysis of capture–recapture models. *J. Ornithol.* 152, 521–537.
- Schoener, T.W., 1974. Resource partitioning in ecological communities. *Science* 185, 27–39.
- Smith, R.B., Peery, M.Z., Gutiérrez, R.J., Lahaye, W.S., 1999. The relationship between spotted owl diet and reproductive success in the San Bernardino Mountains, California. *Wilson Bull.* 111, 22–29.
- Smith, W.P., 2007. Ecology of *Glaucomys sabrinus*: habitat, demography, and community relations. *J. Mammal.* 88, 862–881.
- Smith, W.P., Gende, S.M., Nichols, J.V., 2005. The northern flying squirrel as an indicator species of temperate rain forest: test of an hypothesis. *Ecol. Appl.* 15, 689–700.
- Stephens, S.L., Bigelow, S.W., Burnett, R.D., Collins, B.M., Gallagher, C.V., Keane, J., Kelt, D.A., North, M.P., Roberts, L.J., Stine, P.A., et al., 2014. California spotted owl, songbird, and small mammal responses to landscape fuel treatments. *BioScience*, <http://dx.doi.org/10.1093/biosci/biu137>
- Stephens, S.L., Fry, D.L., Franco-Vizcaino, E., Collins, B.M., Moghaddas, J.M., 2007. Coarse woody debris and canopy cover in an old-growth Jeffrey pine-mixed conifer forest from the Sierra San Pedro Martir, Mexico. *Forest Ecol. Manag.* 240, 87–95.
- Stephens, S.L., Mclver, J.D., Boerner, R.E.J., Fettig, C.J., Fontaine, J.B., Hartsough, B.R., Kennedy, P.L., Schwillk, D.W., 2012. The effects of forest fuel-reduction treatments in the United States. *BioScience* 62, 549–560.
- USDA, 2004. *Sierra Nevada Forest Plan Amendment Final Supplemental Environmental Impact Statement*. USDA Forest Service, Pacific Southwest Region.
- Vanderwel, M.C., Malcolm, J.R., Caspersen, J.P., Newman, M.A., 2010. Fine-scale habitat associations of red-backed voles in boreal mixedwood stands. *J. Wildl. Manag.* 74, 1492–1501.
- Van Horne, B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manag.* 47, 893–901.
- Waddell, K.L., 2002. Sampling coarse woody debris for multiple attributes in extensive resource inventories. *Ecol. Indic.* 1, 139–153.
- Zielinski, W.J., Duncan, N.P., Farmer, E.C., Truex, R.L., Clevenger, A.P., Barrett, R.H., 1999. Diet of fishers (*Martes pennanti*) at the southernmost extent of their range. *J. Mammal.* 80, 961–971.