Mechanisms driving postfire abundance of a generalist mammal

R. Zwolak, D.E. Pearson, Y.K. Ortega, and E.E. Crone

Abstract: Changes in vertebrate abundance following disturbance are commonly attributed to shifts in food resources or predation pressure, but underlying mechanisms have rarely been tested. We examined four hypotheses for the commonly reported increase in abundance of deer mouse (*Peromyscus maniculatus* (Wagner, 1845)) following forest fires: source–sink dynamics, decreased predation, increased food resources, and increased foraging efficiency. We found that reproduction of deer mouse was considerably higher in burned versus unburned forests and survival did not differ between habitats, indicating that burned forests were not sink habitats. Comparable survival also suggested that predation rates were similar between habitats. Increased reproduction in burned versus unburned forest suggested better resource conditions, but abundance of seeds and arthropods (the primary food resources for mice) either did not differ between habitats or were higher overall in unburned forest. Foraging experiments indicated that seed removal from depots was substantially higher in burned versus unburned forests after controlling for mouse density. Additionally, in both habitats, mice were captured more often in open microhabitats and the odds of individual insect removal increased with decreasing cover during certain sampling periods. Of the four hypotheses tested, greater foraging efficiency provided the best explanation for elevated populations of deer mouse. However, predation risk may have influenced foraging success.

Résumé : Les changements d'abondance des vertébrés après les perturbations sont généralement attribués à des modifications dans les ressources alimentaires ou dans la pression des prédateurs; les mécanismes sous-jacents n'ont, cependant, que rarement été évalués. Nous examinons quatre hypothèses pour expliquer l'augmentation d'abondance des souris du crépuscule (*Peromyscus maniculatus* (Wagner, 1845)) couramment signalée à la suite d'un incendie de forêt: la dynamique source-puits, la prédation réduite, les ressources alimentaires accrues et l'efficacité plus grande de la recherche de nourriture. La reproduction des souris du crépuscule est beaucoup plus importante dans les forêts brûlées par comparaison aux non brûlées et la survie ne diffère pas entre les habitats, ce qui indique que les habitats de forêts brûlées n'agissent pas comme des puits. La survie semblable laisse aussi croire que les taux de prédation sont similaires dans les deux habitats. La reproduction accrue dans la forêt brûlée par rapport à la non brûlée indique de meilleures conditions des ressources, mais l'abondance des graines et des arthropodes, les ressources alimentaires principales des souris, ou bien ne diffère pas entre les habitats ou alors est en général plus grande dans la forêt non brûlée. Des expériences de recherche de nourriture montrent que les retraits de graines des dépôts sont considérablement plus élevés dans les forêts brûlées que dans les forêts non brûlées, une fois qu'on a tenu compte de la densité des souris. De plus, dans les deux habitats, les souris sont capturées plus fréquemment dans les microhabitats ouverts et la probabilité du retrait d'un insecte individuel augmente en fonction inverse du couvert durant certaines périodes d'échantillonnage. Des quatre hypothèses testées, l'efficacité accrue de la recherche de nourriture représente la meilleure explication des populations plus élevées de souris du crépuscule. Cependant, le risque de prédation peut avoir influencé le succès de la recherche de nourriture.

[Traduit par la Rédaction]

Introduction

Understanding the factors that influence vertebrate population dynamics is fundamental to animal ecology. Numerous regulatory mechanisms have been considered to explain vertebrate population dynamics (e.g., Chitty 1967; Boonstra 1994; Wolff 1997), but food availability and predation are the most frequently invoked (Erlinge et al. 1983; Messier 1994; Sinclair 2003). Although natural disturbances are known to commonly initiate changes in vertebrate populations (e.g., Karr and Freemark 1985; Pilliod et al. 2003; Fisher and Wilkinson 2005), the specific mechanisms for these changes are rarely identified. One of the more prominent examples of this involves the deer mouse (*Peromyscus*

Received 14 April 2011. Accepted 14 October 2011. Published at www.nrcresearchpress.com/cjz on 20 December 2011.

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doi:10.1139/Z11-111

maniculatus (Wagner, 1985)), a generalist rodent that is widespread in North America. Studies have long shown that populations of deer mouse increase following wildfires in both forests (e.g., Krefting and Ahlgren 1974; Crête et al. 1995; Zwolak 2009) and grasslands (Kaufman et al. 1988; Reed et al. 2005), but the causes for these increases are not known.

High postfire abundance of deer mice has been hypothesized to result from source–sink dynamics (sensu Pulliam 1988; Van Horne 1983): forest fires reduce the quality of habitat of deer mouse, thereby creating population sinks overflowing with surplus individuals from highly productive unburned forest (for examples of high density small-mammal population sinks see Van Horne 1983). If this were the cause of increased mouse densities, we expected that survival and (or) fecundity of mice would be higher in unburned compared with burned forest. Patterns of mouse population parameters in a very similar system were inconsistent with this mechanism (Zwolak and Foresman 2008), but here we revisit this question in the context of competing hypotheses.

Alternatively, fires could improve certain aspects of the habitat of deer mouse. Predation is known to influence rodent population dynamics (Hanski et al. 2001). Thus, postfire population increases could reflect declines in predation pressure. However, very little is currently known about how predators respond to forest fires (Fisher and Wilkinson 2005). If reduced predation were responsible for increased postfire abundance of mice, higher survival of mice would be expected in burned compared with unburned forest. Furthermore, predation strongly affects rodent habitat selection (Brown 1988). In particular, rodents avoid open areas in habitats if the risk of predation is high (Longland and Price 1991; Lagos et al. 1995). Therefore, if reduced predatory pressure were responsible for postfire increases in mice, we expected differential selection for open microsites in burned versus unburned forest.

On the other hand, several researchers have suggested that the postfire increase in abundance of deer mouse reflects an increase in food resources. Although deer mice eat a variety of food items, arthropods and seeds consistently dominate their diet (Martell and Macaulay 1981; Wolff et al. 1985, Pearson et al. 2000). Thus, if the postfire increase in populations of deer mouse results from increased abundance of food resources in burned forest, we expected that burned forest would have more seeds and (or) arthropods, particularly of taxa commonly consumed by deer mice, e.g., Coleoptera, Orthoptera, and Arachnida (D.E. Pearson, unpublished data), relative to unburned forest. In addition, we expected that if more food were available, reproduction of deer mouse in burned stands would also increase given that experimental food additions (Galindo-Leal and Krebs 1998; Banks and Dickman 2000; Díaz and Alonso 2003) and natural food pulses (Pucek et al. 1993; Marcello et al. 2008) often trigger an increase in rodent reproductive activity.

However, food availability is also a function of foraging success, which may be higher in burned forest owing to simplification of habitat structure. In many species, individuals are known to select habitats with low structural complexity because it improves their foraging success (e.g., Parrish 1995; Hill et al. 2004; Warfe and Barmuta 2004). Several studies that have shown deer mice select open microhabitats in grasslands have hypothesized that this is due to increased foraging efficiency associated with reduced vegetative cover (Kaufman et al. 1988; Pearson et al. 2001; Reed et al. 2005). Thus, fire may allow for increased foraging efficiency by simplifying habitat structure, even if resource abundance does not differ between habitats. If habitat simplification conferred such an advantage, we expected that deer mice would select open as opposed to densely vegetated microhabitats, and that mice would remove more food items from open than from densely vegetated microhabitats. Furthermore, if higher foraging efficiency explains the postfire increase in deer mice, more food items should be consumed in burned than in unburned forest. As with the increased food resources hypothesis, increased foraging success would most likely lead to higher mouse abundance through increased reproduction.

Of these hypotheses, only source–sink dynamics has been formally tested (Zwolak and Foresman 2008), and no single study has attempted to address all these hypotheses. We investigated populations of deer mouse in recently burned and unburned montane forest and collected observational and experimental data on the availability of food resources, microhabitat selection, foraging behavior, and demography of deer mouse to assess these possible explanations for postfire increases in abundance of deer mouse. We note that not all hypotheses are mutually exclusive, but testing them simultaneously offers the best means for evaluating the relative viability of each.

Materials and methods

Study area

We conducted this study in west-central Montana, USA, in an area approximately 50 km west of Missoula, Montana, that burned in 2005 by a wildfire. We selected six study sites, three that were burned with a stand-replacement fire and three in adjacent unburned forest. The forest was dominated by Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco), with western larch (*Larix occidentalis* Nutt.), lodgepole pine (*Pinus contorta* Douglas ex Loudon), and ponderosa pine (*Pinus ponderosa* Douglas ex P. Lawson & C. Lawson) present. The study sites were west- or south-facing, located at elevations ranging from 1600 to 1900 m, and at least 0.85 km apart to preclude movement of deer mice among the sites (throughout the study, only one individual was captured at two different sites).

Live-trapping

We trapped mice during summers of 2006 and 2007 in monthly sessions (June–August). Sites were divided into three pairs consisting of one unburned and one burned site, and sites within each pair were trapped simultaneously. Each trapping session consisted of 4 consecutive trap-nights (the only exception was the August 2007 trapping session at sites C3 and F3, which was ended after 3 nights because of adverse weather). At each study site, we set out 169 Sherman live traps in a 13 × 13 grid with 10 m trap spacing. The traps were baited with oats and supplied with polyester bedding. We opened the traps at 1800–1900 and closed them by 1000. We marked each captured rodent with a uniquely numbered ear tag (Monel #1005; National Band and Tag Co., Newport, Kentucky, USA), and recorded its species, mass, and sex. For captured deer mice, we also recorded reproductive condition (animals were considered breeding when females were pregnant or lactating and when males had scrotal testes), and age (juvenile, subadult, or adult; based on pelage color as in Zwolak and Foresman 2008). Shrews were released unmarked. Our research was approved by the University of Montana Institutional Animal Care and Use Committee.

Food resources: seed and insect sampling

To assess food resources of deer mouse, we sampled the seed bank and measured relative abundance of ground-active arthropods in burned and unburned forest. Soil seed bank samples were taken in June and August 2006 and 2007. Each time, we collected soil cores (Newton 2007) from 12 randomly selected points within each trapping grid using a standard 5 cm × 15 cm bulb planter. The samples were sifted and seeds counted and identified to species. We captured arthropods in 10 pitfall traps (10 cm diameter) located randomly within each sampling grid and provided with 60% ethanol as the preservative. This method effectively samples surface-dwelling, cursorial arthropods (Southwood and Henderson 2000), thus it successfully targets most invertebrates that are commonly eaten by deer mice, except lepidopteran larvae (Pearson and Fletcher 2008). Pitfall traps were left open for 2 weeks in July 2006 and 2007 and checked weekly. We identified collected arthropods to order and measured body length to the nearest 0.01 mm.

Microhabitat

In July 2006 and 2007, we visually estimated ground cover (%) of microhabitat variables in 2 m radius plots centered at trap stations within each grid (n = 169 plots/grid) to allow assessment of microhabitat selection by deer mice. Habitat variables were as follows: open area (unvegetated and no debris), herbaceous vegetation (grass and forbs), coarse woody debris (downed logs >5 cm in diameter), and shrubs. We focused on these variables because they have often been found to influence small-mammal habitat selection (e.g., Pearson et al. 2001, Smith and Maguire 2004, Coppeto et al. 2006).

Foraging on tethered insects and single seeds

To assess foraging success in different microhabitats, we measured removal rates of tethered insects and marked conifer seeds at trapping stations. We conducted two single-day trials in mid-June and mid-July 2007, sampling one pair of sites per night. The insects (commercially available field crickets, *Gryllus bimaculatus* De Geer, 1773) were attached with 0.2 mm filaments (50 cm length) looped around their necks and tied to wire flags marking trapping stations (Belovsky et al. 1990, Hedrick and Kortet 2006). A study testing this method concluded that crickets tied for short periods of time (such as in our study) cannot bite through the tether and escape (Hedrick and Kortet 2006). For these trials, we used every second trap station (20 m spacing). At sunset, we tethered 20–30 insects per site (in later trials, growing experience enabled us to tether more insects before dark), and predation rates were examined by 0800. Missing crickets were considered predated. In most cases, the line was cut, presumably by the predator, and in some instances we discovered uneaten remains of tethered crickets (usually heads). Our observations and trapping data indicate that deer mice were the most common insectivores at our study sites. Predation by birds could not be entirely ruled out, but crickets were mostly out at night when birds were inactive and no bird predation was observed.

Conifer seeds were set out and examined at the same time as crickets, but at alternate trapping stations. At each selected station, two seeds (one ponderosa pine and one Douglas-fir) were left on the ground surface and marked with toothpicks located 10 cm below each seed. Seeds in each pair were placed about 1.5 m from one another. Each trial involved setting out 20–30 seeds of each species at every site.

Foraging on seed offerings

In a companion study (Zwolak et al. 2010), we evaluated the level of seed predation in burned and unburned forest using experimental seed offerings. In the present study, we use these data in combination with abundance data of deer mouse to examine per capita foraging efficiency (i.e., seed removal) in burned and unburned habitats. The offerings were presented at the study sites introduced above for 2 days and 2 nights in September 2006 and 2007. Here, we present only the nighttime results because deer mice are rarely active during daytime. Each offering consisted of a Petri dish (150 mm diameter) filled with a mixture of 125 mL sand and 20 seeds (either ponderosa pine or Douglas-fir). Within each trapping grid, we placed 40 seed depots (half with ponderosa pine and half with Douglas-fir seeds) in 20 m intervals at locations corresponding to every other trap station. The offerings were set out 1930–2130 and examined shortly after sunrise (around 0630). In 2007, experiments at the last pair of sites were disrupted by overnight snowfall and so not included the results (see Zwolak et al. 2010).

Statistical analysis

Abundance and apparent monthly survival of deer mice (all age classes combined) were estimated with the program Mark (White and Burnham 1999), separately for 2006 and 2007. We used Huggins closed robust design models (Huggins 1989), following the approach described in Zwolak and Foresman (2008). The competing models, ranked according to their ΔAIC_c values (lower values indicate higher likelihood of a model given the data), are listed in the supplementary Table S1.[1] The estimates were model-averaged to reduce the risk of relying on a single model. The "best" model can vary among data sets, thus model averaging helps to stabilize inference (Burnham and Anderson 2002). The effective sampling area of trapping grids (estimated with mean maximum distance moved (MMDM); White et al. 1982) did not differ between burned (MMDM = 29.0 m, SE = 3.0 m) and unburned forest (MMDM = 33.0 m, SE = 2.3 m; $n_{\text{observations}} = 576$, $n_{\text{individuals}} = 429$, $n_{\text{sites}} = 6$, $t = -1.32$, $P = 0.19$).

The remaining statistical analyses were conducted in R (R Development Core Team 2008), using linear mixed effects models (function "lmer"). The best predictors were identified through backward stepwise elimination of nonsignificant ($P > 0.05$) terms. Interactions between terms were included

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[1] Supplementary materials are available with the article through the journal Web site (http://nrcresearchpress.com/doi/suppl/10.1139/z11-111).

only when they had biological interpretation, i.e., we did not include all possible interactions (e.g., 3- and 4-way) but only those that seemed plausible to explain if they were detected. In each analysis, we included trapping grid (n = 6) as a random effect and fire (burned versus unburned stands) and year (2006 or 2007) as fixed effects. Other explanatory variables were specific to a given analysis and are described below.

Reproductive activity of deer mice (with breeding condition as a binary response variable) was compared between treatments accounting for the effect of month (June, July, and August) as a fixed effect and individual (unique mouse; only adults and subadults included) as a random effect.

Numbers of arthropods (in pitfall traps) and seeds (in soil cores) were modeled using a Poisson distribution, or, if data were overdispersed, a quasi-Poisson distribution. In the later case, we used Markov chain Monte Carlo sampling (function "pvals.fnc") to obtain P values. For analysis of arthropod data, trapping station where a given pitfall was located was entered as a random effect and the week of trapping (first or second) was included as a fixed effect, and observations, as reported in the Results, represent the number of samples collected from pitfalls. In the seed analysis, the month of sampling was included as a fixed effect and observations represent the number of collected soil cores. Arthropod length was log-transformed and modeled using a normal distribution.

To examine microhabitat selection by deer mice, we divided trap stations into those with or without captures in July (when we also sampled microhabitat variables), and conducted logistic regression, beginning with the global model that included microhabitat variables: percentage cover of open area, percentage cover of coarse woody debris, percentage cover of shrubs, numbers of saplings and trees. We did not include percentage cover of herbaceous vegetation because it was highly negatively correlated with open area (r = –0.84). In this analysis, observations refer to the number of trap station measurements.

Removal of seeds from seed trays was analyzed with logistic regression, in two ways. First, we tested whether the probability of foraging on a tray (with exploited trays defined as those missing >1 seed) differed between burned and unburned areas. Second, we tested whether the number of seeds removed from only those trays showing evidence of foraging varied between the two habitats. By doing this, we divided seed removal into two components: encounter rates (first analysis), which is a measure of spatial distribution of foraging, and giving-up densities (second analysis), which measures foraging intensity at a site (see Maron and Pearson 2011). In both analyses, fixed effects included abundance of deer mouse (estimates from August 2006 and 2007) and the night of trial (first or second), and random effects included trapping station.

Foraging on tethered insects and single seeds was analyzed with logistic regression, comparing stations where food was removed (predation event) or not removed. Fixed effects included percentage of open area at a given trap station, month of the experiment (June or July), abundance of deer mouse (estimates from June and July, to control for differences in mouse numbers among trapping grids), and in the case of seed predation, also seed species (ponderosa pine or Douglas-fir), and interactions of the above variables. Trapping station was entered as a random effect to account for the fact that sampling was conducted over two trials per station.

Results

Mouse abundance, survival, and reproduction

Deer mice accounted for 71% of all individuals captured during the study (supplementary Table S2).[1] Other common species included chipmunks (red-tailed chipmunk, *Tamias ruficaudus* (A.H. Howell, 1920), and yellow-pine chipmunk, *Tamias amoenus* J.A. Allen, 1980; the two species were not differentiated in our study), southern red-backed voles (*Myodes gapperi* (Vigors, 1830)), and shrews (genus *Sorex* L., 1758). On average, deer mice were 1.7 times more abundant in burned than in unburned forest (1.6 times more abundant in 2006 and 1.8 times in 2007). However, there was considerable variation in the abundance estimates among time periods and particular sites (Figs. 1*a*, 1*b*). Model-averaged estimates of monthly apparent survival were nearly identical in burned and unburned forest, with widely overlapping standard errors (Fig. 2*a*). However, reproductive activity differed considerably between burned and unburned forest. For males, after accounting for the significant effect of year (the proportion of reproductively active males was higher in 2006 than in 2007) and month (the proportion of males in reproductive condition was higher in June and July than in August), more mice were reproductively active in burned than in unburned forest (56% vs. 36%, 179 individuals, 243 observations, z = 3.35, P = 0.001; Fig. 2*b*). In the case of females, fire was the only significant predictor, with breeding activity higher in burned than inunburned forest (67% vs. 39%, $n_{\text{observations}}$ = 250, $n_{\text{individuals}}$ = 167, z = 4.05, P < 0.0001; Fig. 2*c*).

Relative abundance of seeds and insects

Soil samples collected in unburned forest contained 2.03 ± 0.18 seeds (mean ± SE), whereas those in burned forest had only 0.04 ± 0.02 seeds per sample ($n_{\text{observations}}$ = 288, n_{sites} = 6, z = –6.47, P < 0.0001). Douglas-fir represented 89% and 100% of seeds collected in unburned and burned forest, respectively. Relative abundance of arthropods overall and of Coleopterans did not differ between burned and unburned forest (P > 0.1 in both 2006 and 2007; Fig. 3), whereas that of Arachnida was consistently lower in burned forest ($n_{\text{observations}}$ = 224, n_{sites} = 6; 2006: z = –9.63, P < 0.0001; 2007: z = –4.33, P < 0.0001; Fig. 3). In the first year after fire, the number of Orthoptera in burned forest was low relative to unburned forest (z = –5.12, P < 0.0001), but this pattern disappeared in the second year of the study (z = 0.47, P = 0.64; Fig. 3). The mean body length of arthropods did not differ between burned and unburned forest ($n_{\text{observations}}$ = 17 269, n_{sites} = 6, t = 0.65, P = 0.51).

Microhabitat selection

Capture probability of deer mouse increased with the amount of open area and coarse woody debris (open area: odds ratio = 1.009 per percent cover, $n_{\text{observations}}$ = 2028, n_{sites} = 6, z = 3.61, P = 0.0003; woody debris: odds ratio = 1.031 per percent cover, z = 3.93, P < 0.0001). This pattern did not differ between burned and unburned forest (open area × fire interaction: z = –0.39, P = 0.70; coarse woody

Fig. 1. Changes in the mean abundance of deer mice (*Peromyscus maniculatus*) at trapping grids located in burned (solid line) and unburned (broken line) forest during summer 2006 (*a*) and 2007 (*b*). The whiskers represent standard errors.

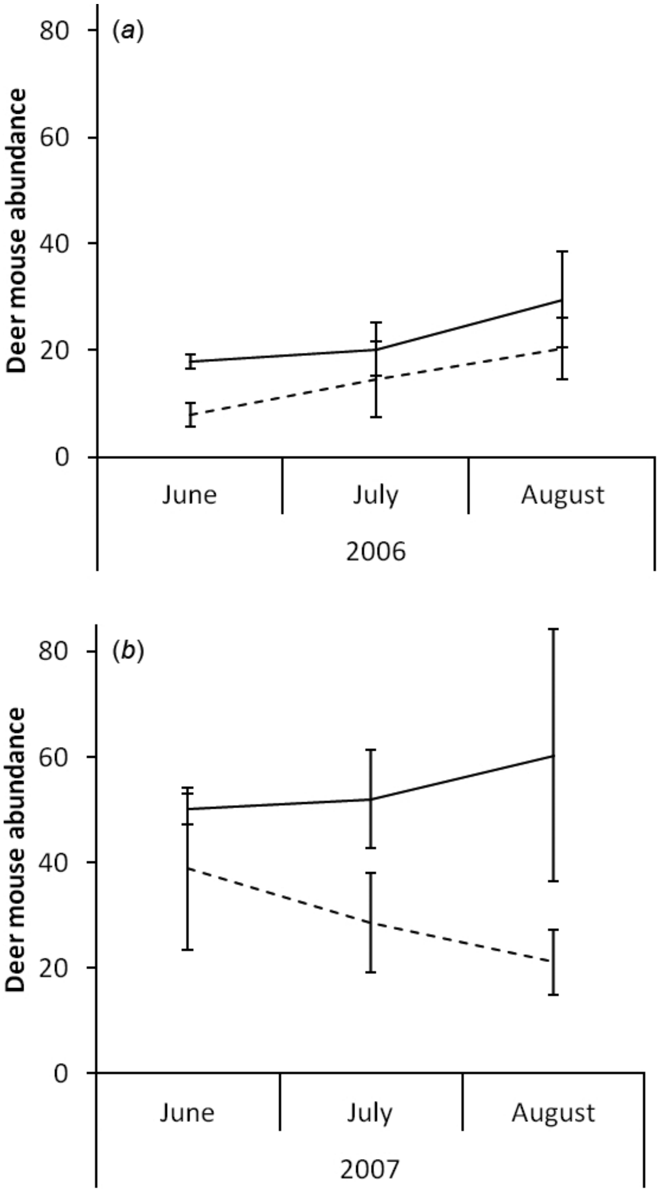
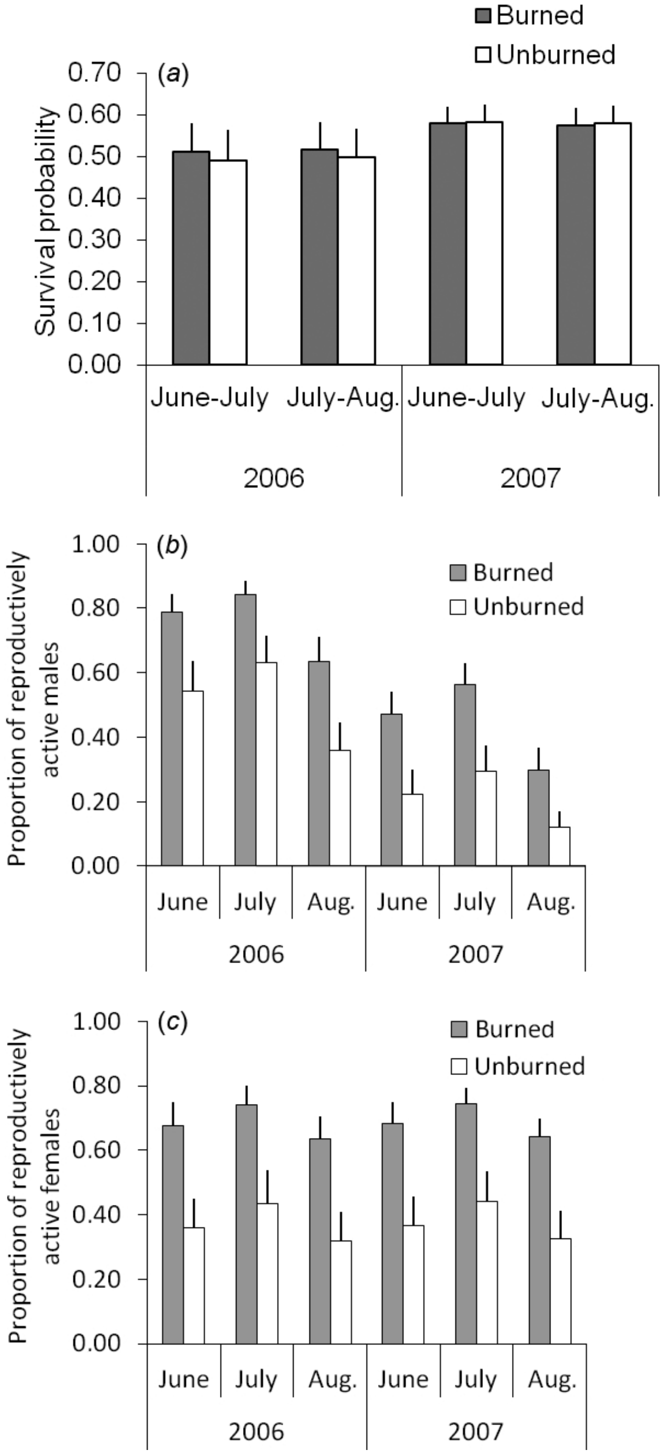
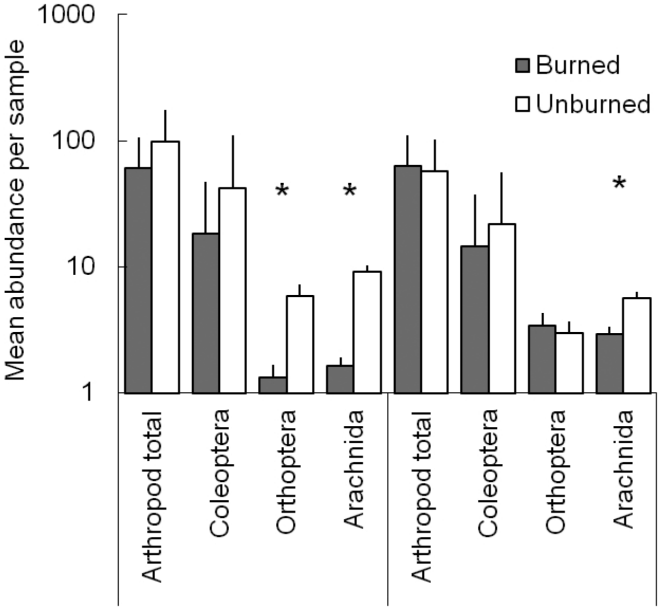


Fig. 2. Demography of deer mouse (*Peromyscus maniculatus*) in burned and unburned forest: (*a*) model-averaged estimates of apparent monthly survival, derived from the program MARK, (*b*) proportion of reproductively active males, and (*c*) proportion of reproductively active females. Bars denote unconditional standard error.



debris × fire interaction: $z = 0.49$, $P = 0.63$). Selection for shrubs differed between burned and unburned forest (shrubs × fire interaction: $z = -2.11$, $P = 0.035$). In unburned forest, deer mice capture probability tended to be higher in areas with higher shrub cover, but this trend was only marginally significant (odds ratio = 1.008, $z = 1.88$, $P = 0.059$). In burned forest where shrubs were rare (supplementary Fig. S1),[1] shrub cover did not influence the probability of capture of deer mouse ($z = -1.57$, $P = 0.12$). Not surprisingly, the probability of capture per station was strongly influenced by the abundance of deer mice at a given site ($z = 10.32$, $P < 0.0001$). Of those variables influencing habitat selection, open area was more prevalent in burned forest (2006: $t = 4.98$, $P < 0.0001$, 2007: $t = 2.58$, $P = 0.01$; supplementary Fig. S1[1]) and shrub cover was less prevalent (2006: $t = -2.90$, $P = 0.004$, 2007: $t = -2.73$, $P = 0.006$; supplementary Fig. S1[1]), whereas the amount of coarse woody debris did not differ between burned and unburned forest ($P > 0.1$; supplementary Fig. S1[1]).

Fig. 3. Numbers of arthropods captured in pitfall traps in burned and unburned forest (samples represent captures in one pitfall over 1 week). Bars denote standard error and significant differences are marked with an asterisk.



Foraging on tethered insects and single seeds

When controlling for the abundance of deer mouse, insects were more likely to be removed from open areas, with odds of removal increasing 1.020 times with every additional percent open area ($z = 2.13$, $P = 0.033$), but this effect occurred only in June trials (month × open area interaction, $z = -2.00$, $P = 0.046$). Fewer tethered insects were depredated in June than in July (30% vs. 64%, $n_{\text{observations}} = 335$, $n_{\text{trap stations}} = 48$, $n_{\text{sites}} = 6$, $z = 3.81$, $P = 0.0001$).

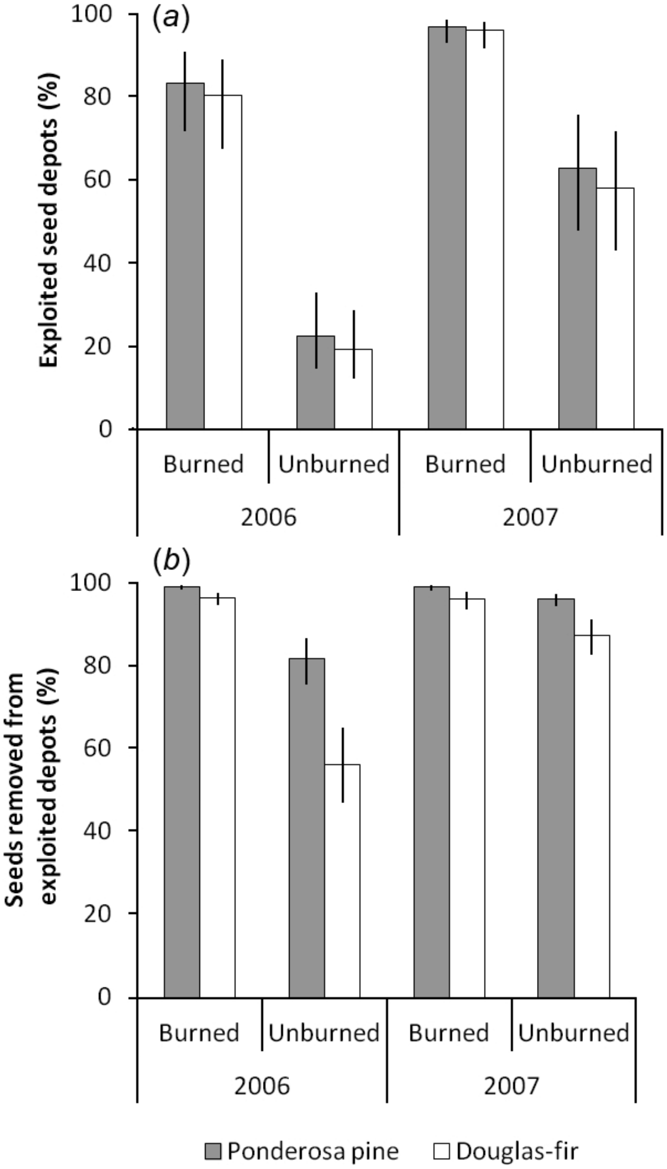
When controlling for the abundance of deer mouse, the probability of single seed removal marginally decreased with the increase in percent open area (odds ratio = 1.009, $z = 1.78$, $P = 0.081$), but this effect occurred only in July trials (month × open area interaction: $z = 2.74$, $P = 0.006$). The magnitude of single seed removal was lower in June than in July (34.2% vs. 39.0%, $n_{\text{observations}} = 648$, $n_{\text{trap stations}} = 52$, $n_{\text{sites}} = 6$, $z = 2.82$, $P = 0.005$). Removal rates did not differ between ponderosa pine and Douglas-fir seeds ($P > 0.1$) and the corresponding variable was removed from the final model.

Foraging on seed trays

More trays experienced seed removal in burned than in unburned forest ($z = 4.71$, $P < 0.0001$; Fig. 4*a*) when controlling for abundance of deer mouse. In addition, more trays were exploited on second compared with the first night of trials ($z = 3.19$, $P = 0.001$), and in 2007 than in 2006 ($z = 6.79$, $P < 0.0001$). Seed species did not influence the probability of tray exploitation ($z = 1.02$, $P = 0.306$).

When controlling for abundance of deer mouse, more seeds were removed from exploited trays in burned than in unburned forest (2006: $z = -2.98$, $P < 0.0001$; 2007: $z = -2.34$, $P = 0.019$; Fig. 4*b*), suggesting that mice foraged more intensively in burned forest. The strength of this effect was greater in 2006 than in 2007 (fire × year interaction, $z = 5.75$, $P < 0.0001$). More ponderosa pine seeds were removed from trays than Douglas-fir seeds ($z = 5.86$, $P < 0.001$).

Fig. 4. Per capita (estimates controlled for differences in abundance of deer mouse (*Peromyscus maniculatus*)) seed depot encounter rates (*a*) and percentage of seeds removed from exploited depots (*b*). The estimates and associated standard errors (denoted by whiskers) were calculated by setting each group, in turn, to be the reference (intercept) group in function lmer in R.



Discussion

We found that deer mice were almost twice as abundant in recently burned forests compared with unburned forests. This increase following fire is moderate compared with some studies. For example, Zwolak and Foresman (2008) found that mice were almost 4 times more abundant in burned than unburned forest, and Krefting and Ahlgren (1974) reported nearly 10-fold higher numbers of deer mice in burned forest. Although this pattern of increase in populations of deer mouse is widely reported and many have speculated as to why it happens (Krefting and Ahlgren 1974; Crête et al.

1995; Zwolak and Foresman 2008; Zwolak 2009), few studies have attempted to examine the underlying causes (Zwolak and Foresman 2008). This is the only study to examine multiple hypotheses for this phenomenon.

Small-mammal studies were among the first to empirically illustrate that high population densities could mask sink populations (Van Horne 1983). For example, Van Horne (1983) attributed elevated populations of deer mouse in timber stands of lower habitat quality to mice overflowing from adjacent source populations. Our findings of higher reproductive activity and comparable survival of deer mice in burned relative to unburned forest do not support the hypothesis that unburned sites function as sources and burned sites as sinks (Pulliam 1988). Zwolak and Foresman (2008) likewise found that burned forest did not serve as sink habitat following wildfire in more mesic forest types.

The hypothesis that higher populations of deer mouse in recently burned stands were due to reduced predation and its positive effect on survival also was not supported. We found no difference in survival of deer mouse between burned and unburned forest. Additionally, analyses indicated no clear pattern of differences in microhabitat selection within burned versus unburned forest that might be attributed to predators. Selection by deer mouse for open areas and coarse woody debris did not differ between burned and unburned forest. There was weak selection for shrub cover in unburned but not in burned forest. This could indicate a greater degree of predator avoidance in unburned forest. However, the lack of response of deer mice to shrub cover in burned forest was not surprising given the low availability of this vegetation type on burned trapping grids. Overall, we found no evidence that predators caused the observed differences in populations of deer mouse between habitats by directly affecting survival of deer mouse.

Our study provided the first direct test of the most commonly invoked explanation for postfire increases in abundance of deer mouse: greater food resources in burned areas (Ahlgren 1966; Krefting and Ahlgren 1974; Nappi et al. 2004). This hypothesis also was not supported by our data. There were considerably fewer seeds and similar or lower abundance of ground-active arthropods in burned versus unburned forest. However, given that our sampling period was limited to mid-summer, we cannot rule out changes in seasonal food resources such as invertebrate populations that might have come and gone outside of our sampling window. It is possible that some highly specialized species such as lepidopterans (not measured in this study) may occur at higher abundances within burned areas if their specific host plants are among the few plant species to increase immediately following fire. However, studies of invertebrates indicate that while responses to fire can be species-specific, most invertebrate populations markedly decline in burned areas (e.g., Paquin and Coderre 1997; Coleman and Rieske 2006; Gillette et al. 2008), particularly after severe fires (Wikars and Schimmel 2001; Saint-Germain et al. 2005). Seed inputs vary seasonally, but seeds should not be so ephemeral that they could not be detected by our sampling methods, which proved sensitive enough to detect differences in conifer seeds between the two habitats. Hence, we found no evidence that food resources were more abundant in the burns where mouse populations increased.

We tested the hypothesis that higher mouse populations in the more open burned stands result from greater foraging efficiency by examining per capita seed removal at seed depots in burned and unburned forest and by evaluating microhabitat selection of deer mouse and its effects on their predation success. Seed tray results indicated that an average mouse (differences in mouse abundance between habitats were controlled for) encountered more seed depots and consumed far more seeds from the depots they encountered in burned habitats than in unburned forest. These results suggest that food consumption may have been higher in burned forest even though resource levels were similar. Additionally, in both habitats, we found that mouse captures were associated with more open microhabitats, consistent with results from numerous other studies and with the prediction that mice may focus on open areas for foraging (Kaufman et al. 1988; Elliott et al. 1997; Pearson et al. 2001; Fuller et al. 2004; Kaminski et al. 2007; but see Goodwin and Hungerford 1979; Morris 2005). Moreover, in half of the foraging trials, the odds of insect predation increased with the amount of open area, though this was not the case for individual seeds. The variability associated with mouse predation success on individual insects and seeds at different microhabitats may be due to our relatively limited sampling effort given the high variability associated with foraging behavior (e.g., Kelt et al. 2004). Overall, our results suggest that higher foraging success in burned forest may have caused the higher reproductive activity that we observed in this habitat, leading to higher population sizes (Galindo-Leal and Krebs 1998; Banks and Dickman 2000; Díaz and Alonso 2003). However, the causes for higher foraging success are not completely clear.

In testing the foraging hypothesis, we assumed that foraging success might be higher in burned forest owing to a greater ability of mice to encounter food resources when habitat complexity is reduced (Kaufman et al. 1988; Pearson et al. 2001; Reed et al. 2005). However, foraging success can also be influenced by competitors and predators (Lagos et al. 1995; Kelt et al. 2004). Competitive interactions are unlikely to explain our foraging results (see below), but predation risk might. Feeding depots can be used to evaluate effects of predators on both local foraging intensity and spatial extent of foraging (Brown 1988). In a grassland system, Maron and Pearson (2011) observed an increase in encounter rates but not in foraging intensity at seed trays on 1 ha grids where all predators were experimentally excluded. Thus, the increased foraging success of mice that we observed in burned forest could have resulted from reduced predation risk, increased encounter rates owing to reduced habitat complexity, or a combination of the two factors (we found no differences in survival of deer mouse in burned and unburned forest, but predation risk still could have differed because it is possible that animals in the safe habitat were out foraging longer). These results suggest that determining what factors influence foraging success of deer mouse may help to understand changes in populations of deer mouse.

An alternative hypothesis is that we simply did not measure the real cause for the postfire increases in populations of deer mouse observed in this study. Some researchers have suggested that changes in mouse abundance may reflect changes in species interactions, particularly interspecific competition or disease. Certain studies suggest that red-backed voles dominate deer mice behaviorally (Crowell and Pimm 1976; Schulte-Hostedde and Brooks 1997), while others challenge this conclusion (Morris 1983, 1996; Wolff and Dueser 1986). Either way, red-backed voles were abundant in only one of our three unburned sites (supplementary Table S2),[1] so changes in their populations cannot explain our results. Shrews are also greatly reduced by fire (Zwolak and Foresman 2007; this study), but evidence for competition between shrews and mice is scarce. Chipmunks tend to be relatively abundant in burned forest (Pearson 1999; Zwolak and Foresman 2007; this study), thus high densities of deer mouse in burned forest cannot be attributed to release from competition with chipmunk species. Alternatively, the increase in abundance of deer mouse in burned areas could be caused by parasite release. Recent studies suggest that parasites can strongly affect the population dynamics of *Peromyscus* species (Pedersen and Greives 2008; Vandegrift et al. 2008), and effects are often mediated through higher reproductive activity in unparasitized mice (Burns et al. 2005; Vandegrift et al. 2008). Wildfires may reduce parasite infestation in birds and mammals (Bendell 1974), suggesting the possibility that deer mice in recently burned areas may be less exposed to parasites and therefore reproduce more intensely. This hypothesis has not been tested. Interestingly, parasite effects on *Peromyscus* species may also interact with food availability (Pedersen and Greives 2008).

A growing body of experimental work suggests that populations of deer mouse and congeneric white-footed mouse (*Peromyscus leucopus* (Rafinesque, 1818)) are insensitive to the top–down effects of predators (Yunger 2004; Maron et al. 2010) but commonly respond to increased food resources (Gilbert and Krebs 1981; Taitt 1981; Jones et al. 1998; Pearson and Fletcher 2008). In examining competing hypotheses for the common phenomenon of increases in population of deer mouse following forest fires, we found evidence that food resources were important, but differential access to food—not differences in food abundance—appeared most important in driving this phenomenon. Moreover, we could not rule out the possibility that predators might have a role in influencing the foraging success of deer mouse and therefore population increases through nonlethal effects on their prey (sensu Preisser et al. 2005). Our results suggest that studies directed at understanding how natural disturbances influence resource availability (not just resource abundance) as a function of foraging behavior and possibly changes in the predator landscape may help to understand patterns of species abundance in nature.

Acknowledgements

We thank L.A. Reynolds and many other University of Montana students for field assistance. R.L. Hutto, K.S. McKelvey, L.S. Mills, and two anonymous reviewers made useful comments on an earlier draft of the manuscript. This project was funded by grants from the USDA Forest Service, Rocky Mountain Research Station, Bitterroot Ecosystem Management Research Project and the McIntire-Stennis Cooperative Research Program; work was conducted while E. Crone was supported by National Science Foundation (NSF) grant DEB 05-15756.

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