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CAUSES AND CONSEQUENCES OF THE POSTFIRE INCREASE  
IN DEER MOUSE (*PEROMYSCUS MANICULATUS*) ABUNDANCE

By

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Dissertation

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for the degree of

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Causes and consequences of the postfire increase in deer mouse (*Peromyscus maniculatus*) abundance

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Wildfire triggers an increase in deer mouse (*Peromyscus maniculatus*) abundance. Here, I describe this phenomenon, investigate its causes, and explore the consequences of the postfire increase in mice for conifer recruitment in burned forest. I documented a shift in small mammal communities away from more specialized species such as red-backed voles (*Myodes gapperi*) and shrews (*Sorex* spp.) and towards greater abundance of generalist deer mice after a wildfire in montane forest. I conducted a meta-analysis of published studies on the abundance of small mammals in disturbed versus undisturbed forests and established that the pattern of increased deer mouse abundance holds for both natural (wildfire) and anthropogenic (different forms of forest harvest) disturbances. However, the postfire increase is significantly stronger than the increase after logging. In another forest wildfire, I tested the four most commonly proposed explanations of this increase: (1) greater abundance of food resources in burned areas, (2) increased foraging efficiency of deer mice, (3) predatory release, and (4) source – sink dynamics, with burned areas acting as high abundance dispersal sink. However, none were supported by data. Thus, I concluded that the existing explanations of postfire increase in deer mouse abundance are unsatisfactory. Finally, I investigated the magnitude and impact of seed predation by deer mice in burned and unburned forest. In seed offerings experiments, overnight conifer seed removal associated with deer mice was more intense in burned than in unburned stands. In germination experiments, emergence of seedlings in cages with openings that allowed access by deer mice was extremely rare in burned and unburned forest. However, in closed cages (deer mice excluded), seedling emergence was low in unburned forest, but considerably higher in burned forest. Wildfire created favorable conditions for seedling recruitment but seed predation by deer mice appeared to remove this advantage.

## PREFACE

My adventure at the University of Montana began with a shrew symposium at the Powdermill Biological Station in Pennsylvania in 2002, where I gave what was probably my worst research talk ever. However, Dr. Kerry R. Foresman saw something behind the bad English, and thanks to him, I enrolled in the Organismal Biology and Ecology graduate program at the University of Montana the following year. When I first arrived to Missoula, the city was completely covered in thick smoke from surrounding forest fires. Fittingly, forest disturbances became the topic of my dissertation research. Working in the fire-shaped landscapes of western Montana completely changed my perception of the ecological role of perturbations like fire. In my home country of Poland, I worked in the last primeval lowland forest in Europe, where fires have been extremely rare and where (as I incorrectly assumed) not much has changed since it served as a hunting ground for Polish kings. Here in Montana, I learned to appreciate the persistent temporal and spatial variability of ecological systems.

One of the most rewarding outcomes of completing my PhD at the University of Montana was being immersed in a very different, but extremely successful, approach to science from that which I had experienced in Poland. Conducting research in the United States proved to be an energetic and exciting enterprise, and I hope to bring some of this spirit back to Poland. Throughout the years, many faculty members at the University of Montana have been a major source of help and inspiration. Dr. Elizabeth E. Crone provided me with continuous encouragement, critical thinking, and infallible logic. I feel extremely fortunate to have had Elizabeth as my advisor. I am deeply grateful to my committee members--Erick Greene, Richard L. Hutto, Kevin S. McKelvey, and L. Scott Mills-- for their constant guidance and patient comments on my clumsy writing. Above all this, they provided me with their unfailing support when I needed it most. Finally, I was fortunate to collaborate with Yvette K. Ortega and Dean E. Pearson, whose ideas and help had a tremendous influence on my research.

I would like to thank Dave Ausband, Julie Beston, Kim Crider, Jason Davis, Martha Ellis, Jennifer Gremer, Rebecca McCaffery, and Nathan Schwab, for being great friends and colleagues. Roni Patrick and Jodi Todd deserve my special gratitude for keeping my research spending under control and for helping me fill out many different but invariably obscure forms. Finally, this research could not have been completed without the persistence of many undergraduate Biology and Wildlife Biology students, who helped me with my fieldwork and various other tasks, for little or no money. I am particularly grateful to those who identified and measured 17,269 badly preserved arthropods – I honestly did not realize that this task would be so dull. Special thanks to Leigh Ann Reynolds, who not only conducted tremendous amounts of fieldwork, but also supported me with her contagious enthusiasm and positive attitude.

This work is dedicated to my parents, Ryszard and Krystyna Zwolak. Their support, patience, and encouragement made this overseas enterprise much easier.

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## GENERAL INTRODUCTION

Disturbances are widely recognized as a crucial component of ecosystem functioning. They create landscape heterogeneity that underlies numerous ecological processes (Turner 2005), influence dynamics of many species (Karr and Freemark 1985), have been traditionally hypothesized to play critical role in determining species richness (Grime 1973; Connell 1978; Huston 1979; Chesson and Huntly 1997), and are increasingly incorporated into biodiversity conservation theory (Attiwill 1994; Wilcox et al. 2006). Moreover, disturbances, by changing habitat structure, resource availability, and species abundances, provide natural “perturbation experiments” that can be used to gain insights into complex ecological systems.

The effects of disturbance on vertebrates have been studied to answer both basic and applied questions (Karr and Freemark 1985; Bury 2004; Schieck and Song 2006). There is evidence that regional faunas are adapted to particular disturbance regimes (Bunnell 1995) and their conservation requires maintenance of a wide spectrum of disturbance types, severities, and frequencies (Hutto 1995). Other than that, few generalizations have emerged so far. For example, Lindenmayer et al. (2008) found that disturbance theory has very limited ability to guide practical management, which should be instead focused on individual species. Still, management based on emulating natural disturbances with timber harvest has gained remarkable support, particularly among foresters (Hunter 1993; Attiwill 1994; Ehnes and Keenan 2002).

For my dissertation research, I examined impacts of forest disturbance on populations, communities, and trophic interactions of small mammals. In chapter 1, I describe changes in small mammal communities after a stand-replacement wildfire in western Montana (Zwolak and Foresman 2007). The fire shifted the communities away from more specialized species such as red-backed voles (*Myopes gapperi*) and shrews (*Sorex* spp.) and towards greater abundance of generalist deer mice (*Peromyscus maniculatus*). To my knowledge, this was the first small-mammal study on the effects of wildfire in a Douglas-fir – western larch forest.

In chapter 2, I use meta-analytic techniques to examine the effects of more types of forest disturbance on small mammal communities in different regions of North

America. My main motivation was to test two very popular views that nevertheless have not been thoroughly assessed: (1) emulation hypothesis: an idea that carefully planned clearcuts may mimic natural disturbances (mostly wildfire) and therefore maintain biodiversity while extracting timber, and (2) the belief that green tree retention harvest mitigates the negative impacts of logging on biodiversity. I demonstrated that (i) the effects of wildfire on small mammal abundance tend to be stronger than those of clearcutting, and (ii) for most investigated small mammal species, the effects of partial harvest did not differ from the impact of clearcutting. Overall, the direction (i.e. increase, decrease, or no change) of the response to forest disturbance was consistent within a species. However, disturbance type influenced the magnitude of this effect, implying that natural and anthropogenic disturbances cannot be treated as equivalent with regard to their effect on wildlife.

One consistent small mammal response apparent both in my study in western Montana (Chapter 1) and from the analysis of published data (Chapter 2) was the post-fire increase in deer mouse abundance. In chapters 3 (Zwolak and Foresman 2008) and 4, I investigate possible causes of this phenomenon. It has been commonly explained as an example of source-sink dynamics, with burned, apparently “destroyed” areas acting as population sinks. In chapter 3, I present data on deer mouse demography and patterns of habitat selection that make evident that this explanation is incorrect. On the contrary, burned areas represent high-quality deer mouse habitat. In Chapter 4, I investigate other possible causes of the post-fire deer mouse increase. As a result of this study, conducted in a different wildfire, I was able to reject other commonly proposed hypotheses, such as increase in food resources (insects and/or seeds) or predator release in burned areas. I found limited support only for an idea that the post-fire simplification of habitat structure improves foraging success of deer mice. However, I cannot exclude the possibility that another, untested hypothesis provides a better explanation of the high abundance of deer mice, or that this phenomenon has multiple, interacting causes.

Finally, in chapter 5 I investigate the consequences of the high post-fire abundance of deer mice for forest regeneration. I demonstrate that seed predation by deer mice may have a dramatic impact on seedling recruitment in burned forests. Using a combination of small mammal trapping and experiments on seed predation and seedling

germination, I establish that the high abundance of deer mice results in intense seed predation, which in turn greatly reduces seedling germination in burned areas. By contrast, when deer mice are excluded, seedling emergence and survival in burned areas is considerably higher than in unburned forest. Thus, even if fire creates favorable abiotic conditions for tree recruitment, seed predation by deer mice obliterates this advantage. I hypothesize that disturbance qualitatively shifts the interaction between deer mice and seedling recruitment. Unburned forests have relatively few mice and extremely few sites for seed germination; caching by mice might actually increase the probability of seed germination and establishment. Burned forests have high mouse densities and good abiotic conditions for germination, so predation clearly negatively affects seedling establishment.

The Addendum consists of a brief review paper covering current ecological and management controversies over forest management in North America. The review, written in Polish, was intended for Polish ecologists, who do not follow the recent developments in the U.S.A. and Canada, but nevertheless are interested in the forest ecology of very distinct, fire-maintained ecosystems of North America.

Chapters 1 and 3 resulted from work conducted under the guidance of Prof. K. R. Foresman, whereas chapters 4 and 5 are an outcome of my collaboration with Drs. D. E. Pearson, Y. K. Ortega, and Prof. E. E. Crone. Together, my dissertation investigates patterns, causes, and certain ecological consequences of disturbance-mediated changes in small mammal communities. I hope that this work will increase appreciation for the critical role of large-scale disturbances in shaping population dynamics and community structure, as well as the ways in which interactions among trophic levels alter the impacts of ecological disturbances.

CHAPTER 1  
EFFECTS OF A STAND-REPLACING FIRE  
ON SMALL MAMMAL COMMUNITIES IN MONTANE FOREST

Abstract: Wildfire, ubiquitous and recurring over thousands of years, is the most important natural disturbance in northern coniferous forest. Accordingly, forest fires may exert a strong influence on the structure and functioning of small mammal communities. We compared the composition of rodent and shrew communities in burned and unburned patches of a Douglas-fir (*Pseudotsuga menziesii*) /western larch (*Larix occidentalis*) forest in western Montana, USA. Trapping was conducted during two consecutive summers after a wildfire. Four trapping sites were sampled in areas that burned at high-severity and two in unburned forest. Small mammal communities in burned sites were characterized by strong numerical dominance of deer mice (*Peromyscus maniculatus*) and greatly reduced proportion of red-backed voles (*Myodes gapperi*) and shrews (*Sorex* sp.). Relatively rare species such as flying squirrels (*Glaucomys sabrinus*) and bushy tailed woodrats (*Neotoma cinerea*) were largely restricted to unburned areas. The numbers of chipmunks (*Tamias* sp.) were similar in burned and unburned areas. Rodent diversity was higher in unburned forest, but only during the first year after fire. Overall, the fire shifted small mammal communities away from more specialized red-backed voles and shrews and towards greater abundance of generalist deer mice.

## Introduction

Over the past few decades, the understanding that recurring disturbance is critical for shaping the structure and function of biological systems has developed into a major ecological paradigm (White and Pickett 1985; Willig and Camillo 1991). In northern coniferous forests, the most important natural disturbance is fire (Ahlgren and Ahlgren 1960; Hansson 1992; Hunter 1993). Fires have been shaping coniferous forest ecosystems for thousands of years (Wein and MacLean 1983; Agee 1993). Nevertheless, most research on the effects of forest disturbances on wildlife has focused on logging and other anthropogenic events, perhaps because natural disturbances such as fire are extremely variable both in space (patchiness) and time (unpredictability), and thus difficult to study. However, fire represents an integral part of an ecosystem that can strongly influence its productivity, diversity and stability (Kilgore 1987). Furthermore, the number and area of wildfires across North America has strongly increased in recent years, partly because of the accumulation of fuels resulting from decades of fire suppression policy (Schoennagel et al. 2004). Consequently, fires have become the focal issue in forest management (National Fire Plan 2000, Healthy Forest Initiative 2002, Healthy Forest Restoration Act 2003 – c.f. Bury 2004) and insights into the effects of fire on wildlife are important for the evaluation of proposed management (Bury 2004).

Due to their abundance and strong ecological interactions, small mammals are important to forest ecosystems (e.g. Maser et al. 1978; Ostfeld et al. 1996). However, very little research has been conducted on the impact of natural disturbances on small mammals in coniferous forest, and a large part of current knowledge comes from studies on the consequences of human-related disturbances such as logging (e.g. Hayward et al. 1999; Sullivan and Sullivan 2001; Klenner and Sullivan 2003; Fuller et al. 2004; Pearce and Venier 2005), clearcutting followed by burning (e.g. Halvorson 1982; Martell 1984; Sullivan and Boateng 1996; Sullivan et al. 1999), or fuel reduction (Converse et al. 2006a, 2006b). In the present study, we compare small mammal communities in unburned and severely burned montane forest, focusing on differences in species composition, diversity, and overall abundance of rodents and shrews. Fire-associated changes in small mammal communities likely depend on time since fire (Smucker et al. 2005), fire characteristics (e.g. severity, size, and timing) and burned forest type (e.g.

species composition and age). Thus, we quantified the vegetation condition in areas trapped, with emphasis on those variables that are considered important for small mammals. To our knowledge, this is the first small mammal study on the effects of wildfire in the Douglas-fir (*Pseudotsuga menziesii*) /western larch (*Larix occidentalis*) forest.

## Materials and methods

### Study site

The study area, Boles Meadow (47°60'N, 113 °45'W), was located in the Seeley valley in west-central Montana (USA), approximately 40 km northeast of Missoula. The topography is hilly, with mean elevation of 1766 m (minimum 1547 m, maximum 1942 m), and mean slope of 13% (SD 6%). The dominant tree species were Douglas-fir and western larch. In August 2003, 4468 acres of forest at Boles Meadow burned in a wildfire caused by a lightning strike. Fire removed all organic material across relatively extensive areas, creating a large-scale mosaic consisting of large, severely burned patches interspersed with smaller areas that burned with lower severity. In May 2004, we selected six study sites: four (F1-F4) within areas burned with very severe, stand replacement fire, and two unburned areas (C1 and C2) within intact forest (the number of sites in burned and unburned forest was unequal because the study design was chosen for a related investigation of the effects of expected salvage logging). At each site, a 1-ha small-mammal trapping grid and three pitfall arrays were constructed. In May 2005, the grids were enlarged to 1.44 ha. The grids were placed more than 0.2 km from the edge of the burn and at median distance of 2.18 km from one another (maximum distance = 5 km). Investigated sites were located at elevations ranging between 1721 m (F4, measured in the center of grid) to 1869 m (C1). All sites were located on south aspects, except for F4 which was located on a north aspect.

### Habitat sampling

We visually estimated percentage vegetation cover in 1-m-radius circles centered at randomly selected trapping stations within each small-mammal trapping site. In 2004, we examined 10 circles per grid. In 2005, we estimated vegetation cover and additionally

measured the volume of coarse woody debris (CWD, defined as downed logs  $\geq 7.5$  cm in diameter,  $\geq 0.5$  m in length) in 28 1-m-radius circles per grid. Volume of each piece of CWD was calculated as  $\Pi \times h \times r \times p$ , where  $h$  is the length of a CWD fragment contained within the circle, and  $r$  and  $p$  are radii at the ends of the CWD piece within the circle. The volume of all CWD within a circle was pooled.

Presence or absence of canopy cover was measured using a moosehorn densiometer (Bonham 1989) along two perpendicular transects per grid that crossed at the center of the grid. In 2004, transects were 90 m long. In 2005, after the grids were enlarged transects were lengthened to 110 m. After the enlargement, the grid centers changed, therefore the transect location changed from year to year. The presence/absence of canopy was recorded at 1-m intervals. Furthermore, we counted trees (more than 2.5 m height) within 1m on both sides of the transects and classified them as either dead or alive. Data from both transects within a grid were pooled and results were expressed as stems/ha.

All vegetation variables were measured in both 2004 and 2005. However, except for changes in the percent vegetation cover (see “Results”), the changes between years were negligible. Therefore, with the exception of vegetation cover, we pooled the data from both years.

### Small mammal trapping

Capture, handling, and marking of all species followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998). In 2004, each of the six grids consisted of 100 trapping stations arranged in a 10 x 10 square at 10 m spacing. In 2005, the grids were enlarged to 144 trap stations (12 x 12). One folding Sherman™ live trap was placed at each station. To protect captured animals from sun and rain, the traps were placed inside open-ended waxed milk cartons or covered with foam sheets. The traps were baited with oats and examined twice daily (morning and evening). A piece of carrot and polyester bedding were placed inside each trap to minimize trapping effects such as weight decline and reduced survivorship (Pearson et al. 2003). Captured rodents were identified to species, weighed, sexed, and individually marked by toe-clipping or ear tagging (species the size of chipmunk [*Tamias* spp] or larger). We did

not attempt to distinguish red-tailed chipmunks (*T. ruficaudus*) and yellow-pine chipmunks (*T. amoenus*) in the field, but in 2005, hair samples were collected from some individuals and their species was determined via genetic analyses (Good et al. 2003).

### Pitfall trapping

To increase the chances of capturing shrews, each live-trapping grid was supplemented with three Y-shaped arrays of pitfalls and drift fences. Each array consisted of four pitfalls (one at the end of each arm and one in the center) connected with 5-m sections of drift fence made of heavy-duty plastic sheeting. The pitfall arrays were smaller versions of the design proposed by Kirkland and Sheppard (1994). The arrays were inspected once a day. Most shrews were found dead, collected and classified to species through skull and dental examination. Shrews found alive were marked by toe clipping and released. Their species was classified as “unknown”.

### Timing of trapping

Live- and pitfall trapping were conducted every third week for four consecutive nights and days. In total, there were eight such trapping sessions per site: four in the summer of 2004 and four in 2005. The only exception was site F3, which was operated for only the first three trapping periods in 2005.

For logistic reasons, trapping sessions could not be conducted at the same time at all sites. To provide valid comparisons between burned and unburned sites, we divided the sites into two sets, each consisting of one unburned and two burned areas. Sites within each set were trapped concurrently. Trapping at sites C1, F1, and F3 began June 1 in 2004 and May 31 in 2005. At sites C2, F2, and F4 trapping began June 8 in 2004 and June 7 in 2005.

### Diversity index

We quantified small mammal diversity using the Simpson index:  $1 - D = 1 - [\sum(p_i^2)]$ , where  $p$  is the proportion of  $i$ -th species among all species captured at a given site. This index was chosen because it de-emphasizes rare detections such as captures of vagrant animals and is easier to interpret and more robust than other widely used indices



(Feinsinger 2001; Magurran 2004). Ninety-five percent confidence intervals (95% CI) for the Simpson index were calculated on the basis of the approach presented in Grundmann et al. (2001), and differences were considered significant when the 95% CI did not overlap.

### Statistical analysis

At several trapping sites, most sampling circles did not contain any vegetation or any CWD, thus the data on these variables could not be normalized. Therefore we used the Mann–Whitney *U*-test to analyze the differences in vegetation cover and CWD between burned and unburned study sites.

In most sampling occasions, small mammals were captured in numbers too small to use abundance estimators (e.g. Pollock et al. 1990). Thus, we used the number of unique individuals captured as an index of abundance. As recommended by McKelvey and Pearson (2001), the chosen method was applied to all compared data.

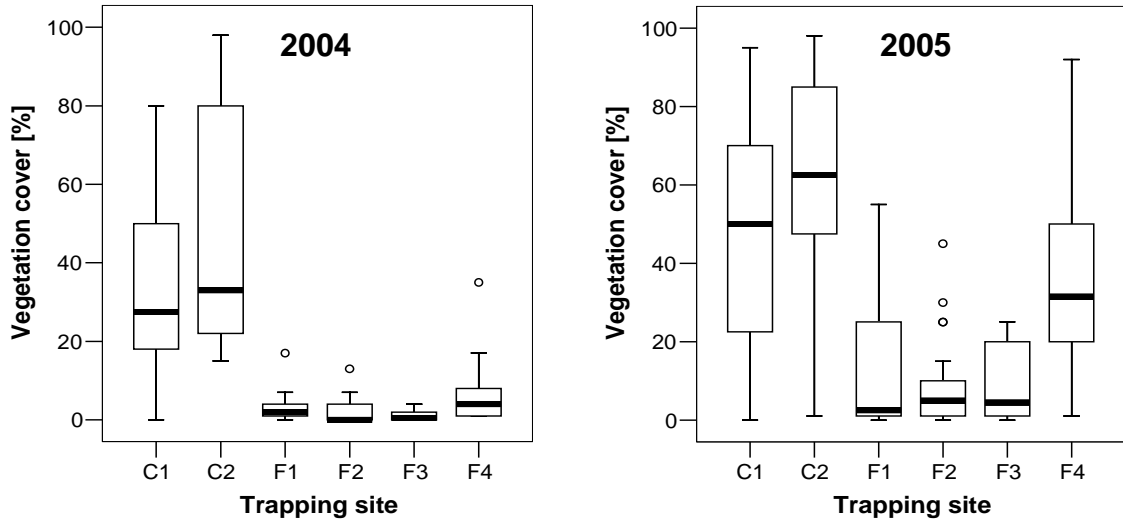
The difference in the number of individuals captured in burned and unburned areas was tested with the “goodness of fit” chi square test or, if less than five animals were captured in either burned or unburned area, Fisher’s exact test (Fisher 1922). If the result was not significant, the “goodness of fit” chi-square test was used to examine if there were differences among particular sites. We used the same procedure to test the hypothesis that the proportion of a given species differs between burned and unburned areas. Significant results were indicated by *P* – values < 0.05.

## Results

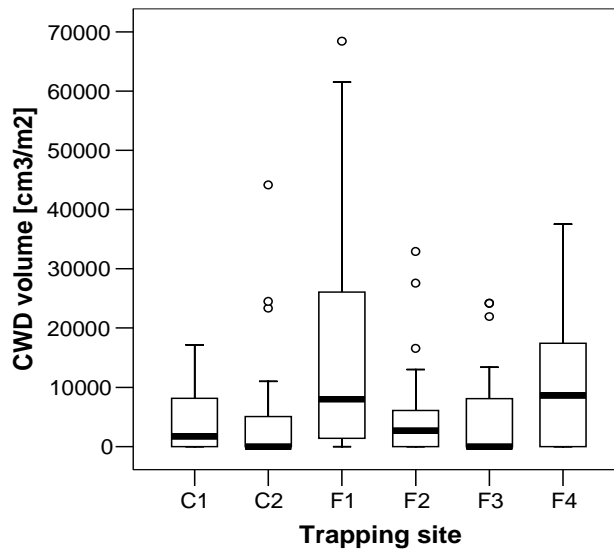
### Vegetation sampling

Tree density averaged 2256 (SE = 456.0) stems/ha in unburned and 2038 (SE = 280.7) stems/ha in burned sites. All trees on the burned sites were killed by fire, whereas in unburned areas, only 12% of trees were classified as dead (none of these were killed by fire). As a consequence, canopy cover at burned areas (13%, SE = 2.1%) was greatly reduced when compared to unburned sites (55%, SE = 6.8%).

Understory vegetation in both unburned areas was dominated by beargrass (*Xerophyllum tenax*) and huckleberry (*Vaccinium sp.*). Most of the vegetation in burned



**Fig. 1.**—Boxplots of percentage vegetation cover in 1m-radius circles centered on randomly selected trapping stations in 2004 ( $n = 10$  circles per each trapping site) and 2005 ( $n = 28$ /site). Boxes denote 25th, 50th and 75th percentiles, whiskers denote the furthest data points within 1.5 interquartile range, and circles denote data points outside of the 1.5 interquartile range.



**Fig. 2.**—Volume of coarse woody debris (CWD) within 1m-radius circles centered on randomly selected trap stations (28 per each trapping site). See Fig. 1 for the explanation of boxplots.

areas consisted of heart-leaved Arnica (*Arnica cordifolia*), fireweed (*Epilobium angustifolium*), and beargrass.

During the first summer after the fire, vegetation cover in burned areas was drastically reduced relative to unburned areas ( $P$ -value  $< .0001$ , Mann–Whitney  $U$ -test). Median percentage vegetation cover in burned sites ranged from 0.5-4%, whereas in unburned areas it varied between 28-33% (Fig. 1). In 2005, median vegetation cover in burned areas increased ( $P$ -value  $< 0.001$ , Mann–Whitney  $U$ -test), ranging from 2.5-31.5%. The fastest regeneration rate occurred at F4, the only north-facing study site. Increase in vegetation cover, however, occurred not only in the burned areas (where it was expected as a result of succession), but also in unburned sites (to 50% at C1 and 62.5% in C2). Still, this increase was not significant ( $P$ -value = 0.113, Mann–Whitney  $U$ -test). In 2005, the differences in vegetation cover between burned and unburned sites, although smaller, remained highly significant ( $P$ -value  $< 0.001$ , Mann–Whitney  $U$ -test).

Fire did not appear to have reduced the amount of CWD (Fig. 2). In fact, the burned areas contained more CWD than unburned ones ( $P$ -value = 0.036, Mann–Whitney  $U$ -test).

### Rodent communities

Relative abundance. Overall, 738 individuals representing 12 species of rodents were caught (Table 1, Plate 1): 10 species were captured in live traps, and an additional 2 species, heather vole (*Phenacomys intermedius*) and northern pocket gopher (*Thomomys talpoides*), were found in pitfalls. During the first year after fire, the relative abundance of rodents differed among sites ( $X^2 = 13.96$ ,  $d.f. = 5$ ,  $n = 464$ ,  $P = 0.016$ ), but not between burned and unburned areas ( $X^2 = 1.81$ ,  $d.f. = 1$ ,  $n = 464$ ,  $P = 0.18$ ). In the second year after fire, even though we enlarged every grid by 44% (see “Methods”), the number of rodents caught was lower at each trapping site (Table 1). During that second year, the relative abundance of rodents was higher in unburned than in burned sites ( $X^2 = 14.45$ ,  $d.f. = 1$ ,  $n = 274$ ,  $P < 0.001$ ).



**Plate 1.**— Selected small mammals captured in Boles Meadow, west-central Montana. Top row: on left deer mouse, *Peromyscus maniculatus* (photo credit K. Ziółkowska), on right chipmunk, *Tamias sp.* (photo credit K. Ziółkowska). Bottom row: on left red-backed vole, *Myodes gapperi* (photo credit L. A. Reynolds) and on right bushy-tailed woodrat, *Neotoma cinerea* (photo credit K. Ziółkowska).

Community composition. Deer mice (*Peromyscus maniculatus*) were invariably the most numerous species in each burned site both years after fire. In 2004, this species represented 64.7% of individual rodents captured in burned sites, and 22.7% of those in unburned areas ( $X^2 = 69.40$ ,  $d.f. = 1$ ,  $n = 464$ ,  $P < 0.001$ ). Similarly, in 2005 deer mice accounted for 61.4% of individuals captured in burned areas, but only 6.6% of rodents in unburned forest ( $X^2 = 86.91$ ,  $d.f. = 1$ ,  $n = 274$ ,  $P < 0.001$ ).

Red-backed voles (*Myodes gapperi*) were abundant in unburned sites, but disappeared almost entirely from the burned sites. In 2004, red-backed voles accounted for 31.2% of individuals captured in unburned areas, but only 2.2% of those captured in burned areas ( $X^2 = 84.60$ ,  $d.f. = 1$ ,  $n = 464$ ,  $P < 0.001$ ). Also in 2005, the proportion of red-backed voles in burned and unburned sites was significantly different (63.6% vs. 8.5%,  $X^2 = 93.13$ ,  $d.f. = 1$ ,  $n = 274$ ,  $P < 0.001$ ).

The proportion of chipmunks did not differ consistently between small mammal communities in burned and unburned areas. One year after fire, chipmunks represented 32.5% of all individuals captured. This proportion differed among sites ( $X^2 = 12.72$ ,  $d.f. = 5$ ,  $n = 151$ ,  $P = 0.026$ ), but not between burned and unburned areas ( $X^2 = 0.45$ ,  $d.f. = 1$ ,  $n = 464$ ,  $P = 0.50$ ). Two years after fire, chipmunks accounted for 20.1% of individuals captured. Again, this proportion differed among sites ( $X^2 = 15.30$ ,  $d.f. = 5$ ,  $n = 55$ ,  $P = 0.009$ ), being higher in burned sites (26.1%) and lower in unburned sites (12.4%). This difference is significant ( $X^2 = 7.96$ ,  $d.f. = 1$ ,  $n = 274$ ,  $P = 0.005$ ), but largely driven by the high number of chipmunks captured at site F4 (Table 1).

Genetic analyses of hair samples collected in 2005 revealed presence of two species of chipmunks, *T. amoenus* and *T. ruficaudus*. Among 14 sampled individuals, nine were identified as *T. amoenus* (four found in unburned and five in burned sites), and five as *T. ruficaudus* (burned areas only). The difference in species composition between burned and unburned sites was not significant ( $P = 0.221$ , Fisher's exact test).

The proportion of bushy-tailed woodrats (*Neotoma cinerea*) was higher in unburned areas than in burned areas (2004:  $P < 0.001$ , 2005:  $P = 0.024$ , Fisher's exact test). However, this result should be interpreted with caution, because this species was captured almost exclusively at site C2. Likewise, flying squirrels (*Glaucomys sabrinus*) represented a higher proportion of the small mammal communities in unburned areas and

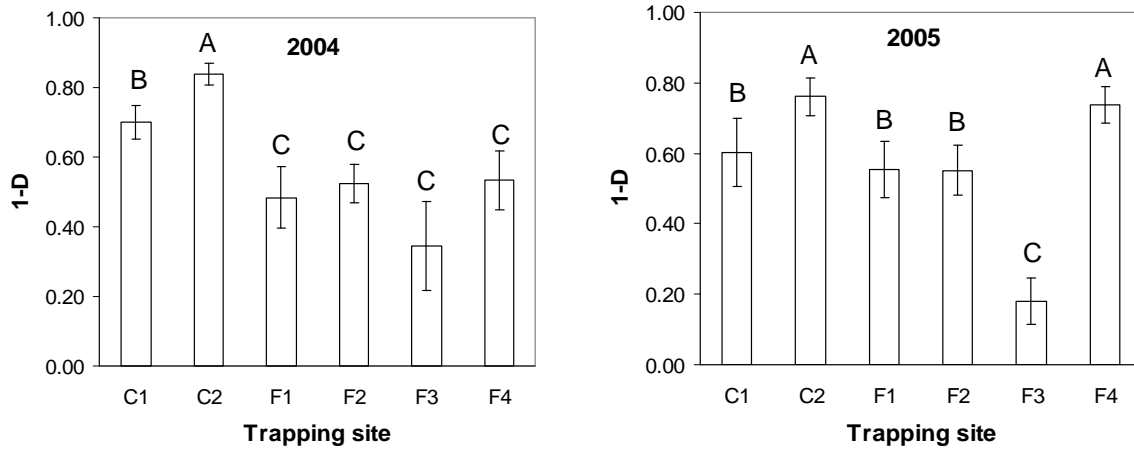
lower in burned areas ( $P = 0.001$  in 2004 and  $P < 0.001$  in 2005, Fisher's exact test), but occurred mainly at C2.

Other species, such as montane voles (*Microtus montanus*), golden-mantled ground squirrels (*Spermophilus lateralis*), Columbian ground squirrels (*Spermophilus columbianus*), red squirrels (*Tamiasciurus hudsonicus*), northern pocket gophers, and heather voles (Table 1), were not captured frequently enough to justify statistical comparisons.

Shrew communities. Overall, we captured 94 shrews (Table 2). In both years, we found 4 species: masked shrew (*S. cinereus*), pygmy shrew (*S. hoyi*), vagrant shrew (*S. vagrans*), and montane shrew (*S. monticolus*). In 2004, we captured 28 shrews in two unburned sites, but only 6 shrews in four burned sites ( $X^2 = 34.62$ ,  $d.f. = 1$ ,  $n = 34$ ,  $P < 0.001$ ). In 2005, the number of different shrews captured equaled 42 in unburned sites and 19 in burned ones ( $X^2 = 34.77$ ,  $d.f. = 1$ ,  $n = 61$ ,  $P < 0.001$ ). The lower overall abundance of shrews in burned sites was primarily caused by the low numbers of masked shrew. This species accounted for 82.1% of all identified shrews captured in unburned sites, but only 56.3% in burned sites ( $X^2 = 4.63$ ,  $d.f. = 1$ ,  $n = 72$ ,  $P = 0.032$ ).

#### Small mammal diversity

One year after fire, diversity ( $1-D$ ) at site C2 was significantly higher than in other areas (Fig. 3). Diversity in burned sites was significantly lower than that in both unburned sites. However, two years after fire the difference between burned and unburned areas was no longer consistent. Diversity at sites C2 and F4 was significantly higher than in other sites, whereas diversity at F3 was significantly lower than that at any other site (Fig. 3).



**Fig. 3.**—The complement of Simpson index ( $1-D$ , estimate and 95% CI) of the rodent communities at different trapping sites in summer 2004 (one year after fire) and 2005 (two years after fire). Indices with non-overlapping 95% CI are marked with different letters.

## Discussion

Our study documents considerable differences in the composition of small mammal communities soon after severe, stand-replacement forest fire that are consistent with expectations based on habitat associations of these species (e.g. Pearson 1999; Foresman 2001; Pearce and Venier 2005). When compared to small mammal communities in unburned forest, those in burned sites were distinguished by much higher proportion of deer mice, substantially lower proportion of red-backed voles and shrews, and almost complete absence of relatively rare species such as bushy-tailed woodrats and flying squirrels. These characteristics were mostly consistent across burned sites and between years. In 2004, the diversity of rodent communities in burned areas was considerably lower than in unburned areas, but this effect disappeared during the second year after fire. On the contrary, the relative abundance of rodents in burned and unburned sites differed during the second, but not the first year after fire.

An increase in deer mice has been reported after very different disturbances in coniferous forest: wildfire (Krefting and Ahlgren 1974; Koehler and Hornocker 1977; Crête et al. 1995), prescribed fire (Bock and Bock 1983), logging (e.g. Martell 1983; Kirkland 1990; Walters 1991; Pearce and Venier 2005), and clearcutting followed by burning (Ahlgren 1966; Halvorson 1982; Martell 1984; Sullivan et al. 1999). The most frequently invoked explanations of this pattern increase involve (1) the increase in food resources in burned forests (insects and/or seed, e.g. Ahlgren 1966) and (2) the creation of dispersal and/or population sinks in disturbed areas (Buech et al. 1977; Sullivan 1979a; Martell 1984; Walters 1991, but see Tallmon et al. 2003).

The avoidance of burned areas by some species of small mammals, including red-backed voles, bushy-tailed woodrats, and flying squirrels, can be attributed to three main factors: (1) reduction in food resources, (2) increased exposure to predation, and (3) distance of the burned plots to potential sources of colonists (>200m) in unburned forest. The strong decline in red-back voles has been reported after various disturbances that result in decreased cover: wildfire (Krefting and Ahlgren 1974; Buech et al. 1977), logging followed by burning (Martell 1984; Halvorson 1982; Walters 1991), and clearcutting (Campbell and Clark 1980; Martell 1982), although this response may be dependent on the size of disturbed patches (Hayward et al. 1999). The avoidance of



burned areas by flying squirrels could also result from their affinity to dense canopy cover for locomotion (Lehmkuhl et al. 2006).

There was no consistent difference in the overall proportion of chipmunks (*T. amoenus* and *T. ruficaudus*) between burned and unburned areas. Both species of chipmunks prefer areas with well-developed understory (e.g. Foresman 2001). Therefore, their abundance after high intensity fire is surprising and may suggest that beneficial effects of fire such as increased availability of seed (Ahlgren 1966) could compensate for the loss of cover.

Data on the responses of shrews to disturbance is very limited because they are rarely caught both in snap- and regular live traps. Moreover, different species of shrews are usually pooled together and treated as identical. In 3 out of 5 studies on clearcutting in coniferous forest reviewed by Kirkland (1990) the abundance of shrews increased after the disturbance. Kirkland (1990) suggested that shrews, as secondary consumers, may be less affected by the changes in plant communities. In the present study, however, the abundance of shrews was greatly reduced in the burned areas. This effect seemed to be driven by the decrease in masked shrew, a species that numerically dominates shrew communities in unburned forest. Similarly, in one of the few studies comparing the responses of different species of shrew to disturbances, Spencer and Pettus (1966) found that the proportion of masked shrew is lower in shrew communities in clearcuts. On the other hand, Crête et al. (1995) and Pearce and Venier (2005) did not detect any change in its abundance after wildfire and clearcutting, respectively, in boreal forest.

The lower abundance of shrews in burned vs. unburned forest could have been caused by the intensity of fire that completely removed not only the vegetation cover, but even the litter layer, and by the subsequent changes in the microclimate. Following tree and shrub destruction, burned forest is much drier than unburned forest (Bendell 1974). Since shrews have high water requirements and are strictly insectivorous, this change may affect them directly or indirectly, by changing the abundance of their prey (Kirkland 1991; McCay and Storm 1997).

### Conclusions

Our study contributes to the growing body of evidence on the role of disturbances in shaping ecosystems, creating habitat heterogeneity, and modifying animal communities. Fire-created mosaic of burned and intact forest supports divergent small mammal communities.

Small mammal communities in burned forest do not contain unique, fire-dependent species, unlike those of plants, insects, or birds. However, the dramatic change in abundances coupled with complete disappearance of some species creates a distinctive community composition that may allow some species to benefit in the short term after fire. Thus, disturbance may contribute to the maintenance of overall diversity across a longer successional span of time.

### Acknowledgements

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**Table 1.**—Number of different individuals of rodent species captured at unburned (C) and burned (F) sites during summer 2004 and 2005.

Species	Trapping grid											
	C1		C2		F1		F2		F3		F4	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
<i>Peromyscus maniculatus</i>	17	1	15	7	51	29	59	25	59	18	40	22
<i>Myodes gapperi</i>	29	50	15	27	1	4	5	1	-	-	1	8
<i>Tamias sp. (2)</i>	39	13	10	2	28	9	34	9	14	2	26	20
<i>Neotoma cinerea</i>	-	-	8	7	-	-	-	-	-	-	1	-
<i>Glaucomys sabrinus</i>	-	3	7	9	-	-	-	-	-	-	-	1
<i>Microtus montanus</i>	-	-	-	-	-	-	-	-	-	-	-	3
<i>Spermophilus lateralis</i>	-	-	-	-	-	-	-	-	-	-	2	1
<i>Spermophilus columbianus</i>	-	-	-	-	1	-	-	-	-	-	-	-
<i>Tamiasciurus hudsonicus</i>	-	2	-	-	-	-	-	-	1	-	-	-
<i>Thomomys talpoides</i>	-	-	-	-	-	-	-	-	-	-	-	1
<i>Phenacomys intermedius</i>	1	-	-	-	-	-	-	-	-	-	-	-
<b>TOTAL</b>	<b>86</b>	<b>69</b>	<b>55</b>	<b>52</b>	<b>81</b>	<b>42</b>	<b>98</b>	<b>35</b>	<b>74</b>	<b>20</b>	<b>70</b>	<b>56</b>

**Table 2.**— Number of different individuals of four species of shrews captured at unburned (C) and burned (F) trapping sites during summer 2004 and 2005. Shrews found alive were marked and released. In these individuals, species remained unidentified.

Species	Trapping site											
	C1		C2		F1		F2		F3		F4	
	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005	2004	2005
<i>S. cinereus</i>	7	14	9	16	-	1	1	3	-	-	-	4
<i>S. hoyi</i>	-	-	3	1	-	-	-	-	1	-	-	-
<i>S. vagrans</i>	2	1	-	-	-	2	-	1	-	-	-	1
<i>S. monticolus</i>	-	1	1	1	-	1	-	1	-	-	-	-
Unknown	4	7	2	1	-	-	2	1	1	2	-	2
TOTAL	13	23	15	19	0	4	3	6	2	2	0	7

CHAPTER 2  
A META-ANALYSIS OF THE EFFECTS OF  
WILDFIRE, CLEARCUTTING, AND PARTIAL HARVEST  
ON THE ABUNDANCE OF NORTH AMERICAN SMALL MAMMALS

Abstract: Wildfires and timber harvest are two of the most important disturbances in North American forests. To evaluate and compare their impact on small mammals, I conducted a meta-analysis on (1) the effect of stand-replacement wildfires and several types of forest harvest (clearcutting followed by burning, clearcutting, and partial harvest) on the abundance of deer mice (*Peromyscus maniculatus*) and red-backed voles (*Myodes gapperi*), (2) the impact of clearcutting and partial harvest on a broader array of small mammal species, and (3) the responses of small mammals to recent and older clearcuts (i.e. less than 10 vs. 10-20 years after harvest). In coniferous and mixed forest, all disturbances except for partial harvest triggered significant increases in the abundance of deer mice and declines in red-backed voles. The increase in deer mice after wildfire was stronger than after either clearcut or clearcut and burned. The abundance of red-backed voles was greatest in undisturbed or partially harvested stands, intermediate after either clearcutting or wildfire, and lowest after clearcutting and burning. While the positive effect of clearcutting on deer mice did not persist beyond 10 years after disturbance, the negative effect on red-backed voles was similar between recent and older clearcuts. In deciduous forest, clearcutting did not result in a consistent change in abundance of deer mice and red-backed voles. For other small mammals, recent clearcutting tended to increase the abundance of yellow-pine chipmunks (*Tamias amoenus*), and meadow and long-tailed voles (*Microtus pennsylvanicus* and *M. longicaudus*). Woodland jumping mouse (*Neozapus insignis*), masked shrew (*Sorex cinereus*), and short-tailed shrew (*Blarina brevicauda*) did not show consistent response to timber harvest. Overall, the impact of different disturbances on the abundance of small mammals (i.e. positive or negative) appears to be species-specific, but disturbance type may influence the magnitude of this effect. Disturbance types can be ranked from severe to mild in terms of small mammal responses.

## Introduction

The structure and function of North American forests has been shaped by natural disturbance, predominantly wildfire (Attiwill 1994). Repeated fire cycles have occurred in many North American forests for thousands of years (Hansson 1992) and forest vertebrates show evidence of adaptation to this disturbance (Bunnell 1995). Currently, forest harvest (mostly in the form of clearcutting) has replaced fire as the primary disturbance in many American forests, causing concerns about loss of biodiversity and resilience of forest ecosystems (Toman and Ashton 1996; Simberloff 1999; Drever et al. 2006). While it is widely accepted that conservation of biodiversity should be one of the primary objectives of forest management (Kohm and Franklin 1997), the means to achieve this goal remain contentious (see e.g. Simberloff 1999).

In recent years, the idea that carefully planned clearcuts could emulate and substitute for natural disturbances (Hunter 1993) has gained remarkable popularity and is promoted as a way to integrate timber production with conservation of biodiversity (Ehnes and Keenan 2002). Still, several researchers have pointed out considerable differences in ecological consequences of fire and logging (e.g. McRae et al. 2001; Hébert 2003; Schieck and Song 2006; Bergeron et al. 2007; Thiffault et al. 2007).

Harvest with retention of green trees (hereafter “partial harvest”) has emerged as a common method to increase ecological sustainability of timber production (Work et al. 2003). Traditionally, the primary goal of partial harvest was to improve post-harvest stand regeneration (e.g. shelterwood or selection systems, Nyland 2002), but currently it is often used to maintain “environmental values associated with structurally complex forests” (variable retention harvest systems, Franklin et al. 1997). However, empirical evidence supporting this use of partial harvest remains scant (Simberloff 2001; Schulte et al. 2006).

In this study, I (1) tested the ecological premise of emulation silviculture using small mammals as model organisms, (2) characterized the response of small mammals to different types of harvesting techniques, and (3) evaluated temporal changes in the abundance of small mammal species in clearcuts. To achieve these objectives, I conducted a meta-analysis on the changes in the relative abundance of small mammals

after wildfire and several types of forest harvest: clearcutting, clearcutting followed by burning, and partial harvest.

Small mammals represent the majority of mammalian species in North American forests and play important roles in the functioning of forest ecosystems (e.g. Maser et al. 1978, Ostfeld et al. 1996, Jones et al. 1998, Tallmon et al. 2003). A relative profusion of small mammal studies enables the use of meta-analytic approach, which offers improved control over type II statistical errors (Arnqvist and Wooster 1995). Furthermore, by synthesizing results of studies conducted on different species, in different areas, and within different timeframes, the scope of inference in meta-analysis can be considerably greater than in the standard single-study approach (Osenberg et al. 1999). Finally, meta-analyses are thought to be more informative and objective than qualitative reviews (Arnqvist and Wooster 1995).

This study consisted of three analyses. First, I compared the effects of stand-replacement wildfires and several types of forest harvest (clearcutting followed by burning, clearcutting, and partial harvest) on the abundance of the two most commonly investigated species, deer mice (*Peromyscus maniculatus*) and red-backed voles (*Myodes gapperi*). This comparison directly addressed the question of whether anthropogenic disturbances emulate natural ones. Second, I quantified the impact of clearcutting and partial harvest on the abundance of a broader array of small mammal species: yellow-pine chipmunk (*Tamias amoenus*), deer mouse, red-backed vole, woodland jumping mouse (*Neozapus insignis*), meadow and long-tailed vole (*Microtus pennsylvanicus* and *M. longicaudus*), masked shrew (*Sorex cinereus*), and short-tailed shrew (*Blarina brevicauda*). This analysis measured relative severity of these types of harvesting techniques according to their influence on small mammals. Third, I examined the temporal dynamics of the effects of clearcutting on all of the above species except yellow-pine chipmunk and long-tailed vole. The goal of the third analysis was to identify species with ephemeral and long-lasting responses to this disturbance. Together, these analyses assessed whether natural and anthropogenic disturbances could be ranked from mild to severe in terms of small mammal response, or whether species/disturbance relationships were unique and idiosyncratic.

## Materials and Methods

### Source Data

The data set used in this meta-analysis consisted of studies reporting the effects of wildfire, clearcutting followed by prescribed burning, clearcutting, and partial harvest on the abundance of North American small mammals (rodents or shrews). The analyzed studies were published between 1970 and 2008. I identified relevant publications by searching online databases of Agricola and the Web of Science (conducted in April 2008) using the following search words: *forest* and (*logging* or *harvest\** or *clearcut\** or *fire* or *wildfire* or *burn\**), and (“*small mammals*” or *rodent\** or *mice* or *mouse* or *vole\** or *shrew\**), and searching bibliographies of the studies that I retrieved.

I selected studies that reported the abundance of small mammals in disturbed and matching undisturbed (control) forest. Because the abundance of small mammals tends to fluctuate from year to year, I included only studies where trapping was conducted simultaneously on disturbed and undisturbed plots. When pre-disturbance data were available, they were examined only qualitatively to ensure that control plots were sufficiently similar to those that became disturbed.

I selected research papers where estimates or indices of abundance were derived from trapping and presented in text, tables, or bar charts. When the same results were presented in several papers, I used the most inclusive version. I did not use live-trapping studies where the number of captures rather than the number of different individuals captured was used. I excluded studies where abundances of related species were pooled because species within the same genus are known to react differently to forest disturbance (e.g. Songer et al. 1997). To avoid confounding effects of patch configuration and edge effects, I did not use data from studies on strip clearcutting, patch clearcutting (clearcuts less than 2 ha), or other logging practices such as aggregated retention harvest (Franklin et al. 1997) that create small-scale mosaic of undisturbed and disturbed forest.

### Calculation of Effect Sizes

Evaluating small mammal abundance requires considerable trapping effort. Therefore most studies in the data set were either unreplicated or contained only 2-3 replicates in each treatment. Furthermore, standard deviations could not be extracted



from most of the studies. Thus, I could not apply commonly used effect sizes that are based on standard deviation and often require sample size greater than 5 or 10 (Rosenberg et al. 2000). Instead, I used the relative abundance index (RAI) developed by Vanderwel et al. (2007):

$$\text{RAI} = (N_{\text{disturbed}} - N_{\text{undisturbed}}) / (N_{\text{disturbed}} + N_{\text{undisturbed}})$$

where  $N_{\text{disturbed}}$  and  $N_{\text{undisturbed}}$  is the abundance reported for disturbed and undisturbed sites, respectively. This index ranges from -1 (species found in disturbed sites only) to 1 (species found only in undisturbed sites).

I selected only those studies where at least 10 individuals were captured in at least one site category (disturbed or undisturbed). To avoid potential bias, I did not use any other inclusion criteria based on study quality (Englund et al. 1999). However, studies that involved more intensive sampling are more likely to yield reliable results. To take this into account, I weighted the effect sizes by the  $\log_{10}$  of the total number of individuals used to calculate given RAI. I chose this conservative weighting scheme because the number of different individuals used to calculate RAI ranged from 10 to 4004.

Some studies did not provide the number of individuals captured or information sufficient to calculate it. In such cases, I tried to contact their corresponding author. For studies where this information proved impossible to obtain, I included only those where in at least one site category standard error of the abundance did not exceed the value of the mean. For such studies, I assumed the lowest acceptable number of captures, thus their weight equaled  $\log_{10}(10) = 1$ .

Studies were divided according to (1) the type of disturbance, (2) time since disturbance, (3) forest type (coniferous, mixed, and deciduous). For each study, I calculated one effect size per species per category (disturbance type, time, and forest type), using abundances averaged across years and replicates.

Disturbances included stand-replacement wildfire, clearcutting followed by broadcast burning, clearcutting, and uniform partial harvest. The last category was the most varied. It included harvest labeled as shelterwood (e.g. Waters and Zabel 1998),

diameter-limit cut (e.g. Ford and Rodrigue 2001), basal area retention harvest (e.g. Elliot and Root 2006), or single-tree selection (e.g. Klenner and Sullivan 2003). Most studies on partial harvest included in this analysis were conducted after removal of 30-60% of basal area (range 29-79%; restricting the analysis to 30-60% of basal area removed did not influence the overall pattern).

Time since disturbance was divided into 2 categories: early (<10 years after disturbance) and late (10-20 years after disturbance) because this grouping was very common among the reviewed studies. Studies reporting a single measure of abundance from a period covering two of the above categories were assigned on the basis of greater overlap (e.g. 8-14 years after logging were assigned to the “10-20 years after” category). Time was calculated since the most recent disturbance (e.g. the date of broadcast burning rather than the date of prior clearcutting). I excluded data collected within the first 3 months since the disturbance to avoid confounding effects of disturbances on habitat with their direct effects on small mammals.

Overall, 52 studies satisfied all the above-listed criteria (see Appendix A).

### Statistical Analysis

To analyze species-specific changes in abundance after forest disturbances, I used a multiple linear regression model with RAI as the response variable and disturbance type (comparison 1), small mammal species and harvest practice (comparisons 2), or small mammal species and time category (comparison 3) as explanatory variables.

In each analysis, normal distribution of errors was assured by examining Q-Q plots and conducting Shapiro-Wilk tests (all  $p$ -values were  $> 0.1$ ). Examination of residuals revealed mild nonconstant variance.  $P$ -values of less than 0.05 were considered “significant” and those between 0.1 and 0.05 “marginally significant”.

To examine the robustness of my findings, I conducted also the Kruskal-Wallis analysis of variance on ranks followed by the Wilcoxon tests on the unweighted data. Qualitative conclusions did not differ from those based on parametric tests with weights (results not shown). All analyses were conducted in R (Ihaka and Gentleman 1996).

Initial data analysis suggested that for deer mice and red-backed voles, the effects of harvest differed between deciduous and coniferous/mixed forests. Therefore, for these

two species, data from deciduous forests were not included in comparisons 1-3 below, but were analyzed separately.

## Results

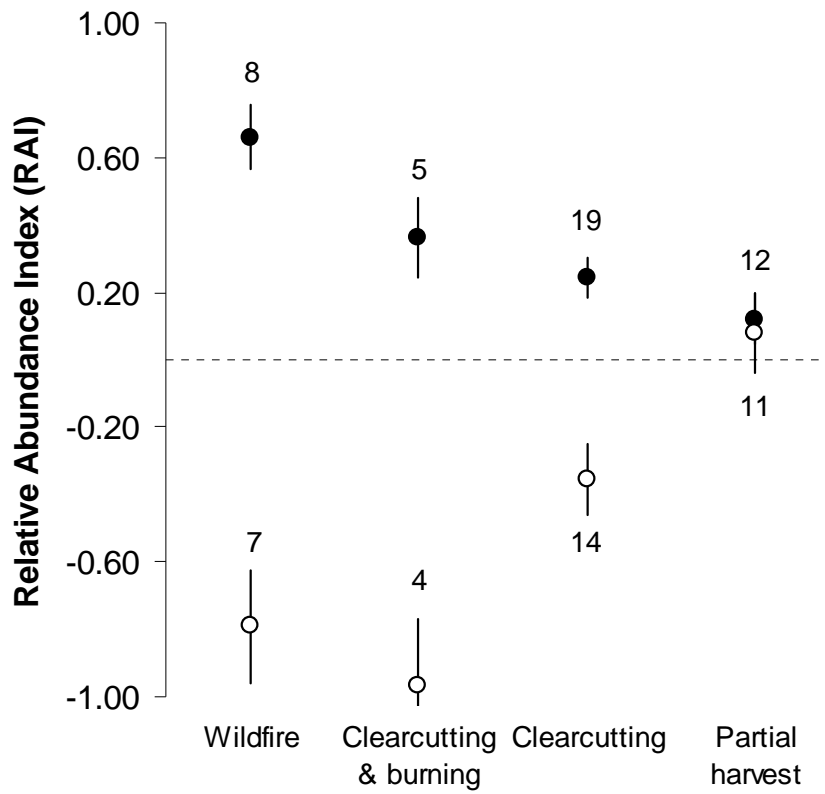
### Comparison 1: Short-term (0-9 years) effects of wildfire and forest harvest in coniferous and mixed forest on deer mice and red-backed voles

Deer mice increased in response to all forest disturbances, but the strength of this response depended on the type of disturbance (Fig. 1). The response to fire was stronger than to any other disturbances: clearcutting followed by burning ( $t_{3,40} = -1.99$ ,  $p = 0.053$ ), clearcutting ( $t_{3,40} = -3.73$ ,  $p = 0.0006$ ), or partial harvest ( $t_{3,40} = -4.43$ ,  $p < 0.0001$ ). The effects of partial harvest did not differ from those of clearcutting ( $t_{3,40} = 1.255$ ,  $p = 0.217$ ).

Red-backed voles decreased in response to all disturbances with the exception of partial harvest (Fig. 1). The effects of clearcutting followed by burning were not significantly different from those of wildfire ( $t_{3,32} = 0.68$ ,  $p = 0.498$ ). The decline in abundance after wildfire was stronger than after clearcutting ( $t_{3,32} = -2.20$ ,  $p = 0.034$ ). For red-backed voles, the impact of clearcutting was significantly different than that of partial harvest ( $t_{1,23} = -2.74$ ,  $p = 0.01$ ).

### Comparison 2: Short-term effects of clearcutting and partial harvest

Yellow-pine chipmunks, deer mice, and both *Microtus* species were significantly more abundant and red-backed voles were significantly less abundant in clear cuts relative to undisturbed areas (Table 1). Partial harvest significantly increased the abundance of yellow-pine chipmunks and marginally significantly increased abundance of meadow voles (Table 1). The responses of other species to either type of forest harvest were not statistically significant and in general, small mammal species responded in a similar way to clear-cutting and partial harvest. Other than the red-backed vole (comparison 1 above), only *Microtus* species showed some evidence of a difference in the response to clearcutting and partial harvest (long-tailed vole:  $t_{111} = -1.95$ ,  $p = 0.053$  and meadow vole:  $t_{111} = -1.80$ ,  $p = 0.074$ ).



**Fig. 1.**—The abundance of deer mice, *Peromyscus maniculatus* (filled circles) and red-backed voles, *Myodes gapperi* (open circles) after stand-replacement wildfire and three types of timber harvest relatively to undisturbed forest. Bars represent standard errors; numbers denote sample sizes.

**Table 1.**—Abundance of small mammals in clear-cut and partially harvested forest relatively to undisturbed forest, 1-9 years after disturbance. *P*-values concern the hypothesis that the relative abundance index (RAI) equals 0.

<i>Species</i>	<i>Harvest type (sample size in parenthesis)</i>	<i>RAI (SE)</i>	<i>t-value</i>	<i>P-value</i>
Short-tailed shrew	Clear-cutting (10)	<b>-0.06</b> (0.12)	-0.47	0.639
	Partial harvest (6)	<b>0.00</b> (0.16)	-0.03	0.980
Red-backed vole	Clear-cutting (14)	<b>-0.35</b> (0.09)	-3.80	0.0002
	Partial harvest (11)	<b>0.08</b> (0.10)	0.76	0.450
Long-tailed vole	Clear-cutting (4)	<b>0.68</b> (0.17)	3.95	0.0001
	Partial harvest (3)	<b>0.10</b> (0.24)	0.44	0.664
Meadow vole	Clear-cutting (11)	<b>0.72</b> (0.12)	6.17	>0.0001
	Partial harvest (5)	<b>0.33</b> (0.18)	1.78	0.078
Woodland jumping mouse	Clear-cutting (6)	<b>-0.07</b> (0.17)	-0.42	0.675
	Partial harvest (3)	<b>0.09</b> (0.26)	0.36	0.722
Deer mouse	Clear-cutting (19)	<b>0.24</b> (0.08)	2.94	0.004
	Partial harvest (12)	<b>0.12</b> (0.10)	1.14	0.257
Yellow-pine chipmunk	Clear-cutting (3)	<b>0.67</b> (0.20)	3.28	0.001
	Partial harvest (5)	<b>0.47</b> (0.17)	2.70	0.008
Masked shrew	Clear-cutting (11)	<b>0.12</b> (0.12)	1.04	0.301
	Partial harvest (3)	<b>0.00</b> (0.23)	-0.02	0.987

### Comparison 3: Long-term effects of clearcutting

10-20 years after clear-cutting, the abundance of deer mice and meadow voles was no longer higher than in undisturbed forest (Table 2). For both of these species, the short-term and the long-term responses to clear-cutting were marginally different (deer mouse:  $t_{98} = 1.77$ ,  $p = 0.079$ ; meadow vole:  $t_{98} = 1.83$ ,  $p = 0.071$ ). There was some indication that at this stage the abundance of woodland jumping mice may be higher in clear-cuts than in undisturbed forest, but the evidence was inconclusive (Table 2). The short- and long-term responses of this species did not differ significantly ( $t_{98} = -1.50$ ,  $p = 0.138$ ). Red-backed voles were negatively affected by clearcutting even in the long term (Table 2). There was no difference between the short-term and long-term response of this species ( $t_{98} = -0.35$ ,  $p = 0.729$ ). Shrews did not show significant long-term response to clearcutting (Table 2) nor any difference between short-and long-term effects (short-tailed shrew:  $t_{98} = -0.20$ ,  $p = 0.887$ ; masked shrew:  $t_{98} = 0.30$ ,  $p = 0.765$ ).

**Table 2.**—Abundance of small mammals in clear-cut areas relatively to undisturbed forest 10-20 years after disturbance.

<i>Species</i> ( <i>sample size in parenthesis</i> )	<i>RAI (SE)</i>	<i>t-value</i>	<i>P-value</i>
Short-tailed shrew (8)	<b>-0.03</b> (0.15)	-0.20	0.846
Red-backed vole (8)	<b>-0.30</b> (0.13)	-2.32	0.023
Meadow vole (4)	<b>0.25</b> (0.23)	1.11	0.270
Woodland jumping mouse (6)	<b>0.33</b> (0.19)	1.72	0.088
Deer mouse (7)	<b>-0.05</b> (0.14)	-0.38	0.707
Masked shrew (6)	<b>0.06</b> (0.17)	0.34	0.737

## Effects of clearcutting in deciduous forest on the abundance of deer mice and red-backed voles

Due to the small number of studies conducted in deciduous forest (6 for each species), only the short-term effects of clearcutting on deer mice and red-backed voles could be analyzed statistically. In contrast to coniferous and mixed forests, clearcutting in deciduous forests did not affect the abundance of these species relative to undisturbed areas (deer mouse: RAI = -0.02, SE = 0.12,  $p = 0.88$ ; red-backed vole: RAI = 0.15, SE = 0.21,  $p = 0.49$ ). The differences between responses in deciduous versus coniferous/mixed forests were marginally significant (deer mouse:  $t_{23} = 1.84$ ,  $p = 0.078$ ; red-backed vole:  $t_{18} = -2.06$ ,  $p = 0.054$ ).

## Discussion

Disturbances clearly differed in their severity as measured by the impact on small mammals. The effects of stand-replacement wildfire were stronger than those of clearcutting, at least for the two most common small mammals: red-backed voles, which tended to decline in abundance after disturbances, and deer mice, which tended to increase. The rank of clearcutting followed by burning was unclear: the effects on the abundance of deer mice were weaker than those of wildfire, but the impact of these two disturbances did not differ for red-backed voles. This lack of resolution may be caused by the low number of small-mammal studies on this kind of disturbance. As expected, partial harvest tended to have weaker effects than clearcutting, but for most small-mammal species this difference was not significant. In general, the responses to these disturbances were characterized by considerable intraspecific variation, which deserves closer scrutiny.

In this analysis, I pooled together different types of harvest under the label of “partial harvest”. While it would be useful to examine how the responses of small mammals change with retention level (as was done for forest birds by Vanderwel et al. 2007), the existing number of studies did not allow this level of resolution. Moreover, small mammal response to a relatively homogeneous harvest method, clearcutting, was similarly varied. These differences are most likely related to variation in certain habitat features, possibly caused by differences in clearcutting techniques (e.g. scarification:

Martell and Radvanyi 1977) and regional climates affecting regeneration rate. The literature on small mammal habitat use in disturbed forest is extensive (see e.g. Pearson 1999; Fisher and Wilkinson 2005 and discussion sections in Klenner and Sullivan 2003; Fuller et al. 2004; Sullivan et al. 2008), but based mostly on correlative evidence. Therefore, it should not be surprising to find numerous contradictory findings. For example, in different studies, deer mice have been found to prefer open areas (Pearson et al. 2001; Fuller et al. 2004; Kaminsky et al. 2007), areas with dense vegetation (Bowers and Smith 1979; Vickery 1981; Kyle and Block 2000; Morris 2005), or not to show any vegetation preferences at all (Smith and Maguire 2004). Clearly, we need more experimental, manipulative studies on small mammal habitat use to be able to better understand their habitat preferences (see e.g. Moses and Boutin 2001; Craig et al. 2006).

The impact of different disturbances on the abundance of small mammals (i.e. increase, decline, or no change) appeared to be species-specific. Species that tended to increase during the first 1-9 years after disturbances included habitat generalists (deer mice and yellow-pine chipmunks) and species that prefer grassy areas and are rarely caught in closed forests (meadow and long-tailed voles). The abundance of short-tailed and masked shrews did not change in response to forest harvest. In the long-term, woodland jumping mice appeared to be positively affected by clearcutting, perhaps because of their association with abundant herbaceous cover that develops after canopy is removed (Miller and Getz 1977; Kaminsky et al. 2007). However, the evidence of positive response was not conclusive.

The only species that was negatively affected by all disturbances except partial harvest was red-backed vole. Moreover, this negative response was lasting, as indicated by the long-term decline in abundance after clearcutting. This result corroborates findings of recent field studies: St-Laurent et al. (2008) concluded that stands of 3 m in height (i.e. 14-17 years after harvest), considered “regenerated” under the legislation of some Canadian provinces, do not maintain abundance of red-backed voles similar to those of unharvested mature forest. Red-backed voles show strong preference for with mesic habitats (Yahner 1986; Morris 1996) and have been proposed as an indicator of mature forest (Nordyke and Burskirk 1988; McLaren et al. 1998; see also Pearce and Venier 2005 for critical evaluation). This analysis shows that this role may be played in



coniferous and mixed forests only. In deciduous forests, the abundance of red-backed voles tended to be similar between clearcuts and mature forests.

The response of deer mice also differed between deciduous and coniferous forest, but for other investigated species forest type did not influence the effects of forest harvest in any perceptible way. This is in agreement with the statement that when assessing the effects of forest harvest, for many species of small mammals “it is apparently not necessary to make a major distinction between coniferous and deciduous forests” (Kirkland 1990), at least until more studies are conducted and higher resolution can be achieved.

The debate over whether forest harvest should emulate severe natural disturbances such as stand-replacement fires, or retain structural features associated with mature forest is still ongoing. The current study indicates that the results of clearcutting, even if it is followed by broadcast burning, differ from those of stand-replacement wildfires. Therefore, emulation of natural disturbance may be problematic. So far, the main focus has been on emulating the shape and size distribution of fires (Hunter 1993). However, if there are intrinsic differences in local habitat quality between burned and clearcut areas, adjusting the shape and size of clearcuts is unlikely to be successful in emulating the effects of fires. Harvest that retains residual structures such as snags and logs is unlikely to increase the similarity between the effects of wildfire and forest harvest because effects of the former on small mammals appear to be *more*, not less severe. The management implications of this analysis are profound: managers need to pay more attention to managing for the maintenance of naturally disturbed (burned) forest conditions because artificial disturbance is clearly not a good substitute.

Studies on other taxa yield similar results. Buddle et al. (2005) found considerable differences between clearcutting and wildfire in the succession rate of arthropod communities. They concluded that the effects of wildfire were more severe than those of clearcutting. Bird communities also differ between stands disturbed by wildfire and forest harvest (Schieck and Song 2006). These differences are very pronounced during the first 10 years after disturbance, tapering off afterwards. However, in contrast to arthropods or birds, there are no fire-dependent species among small mammals in North American forests.

Perhaps the most important question is if the differences in small mammal responses to disturbance affect the functioning of forest ecosystems. Given the commonness of investigated small mammal species, even relatively small changes in their numbers may influence important ecological processes (Gaston and Fuller 2007). For example, Tallmon et al. (2003) found that increased number of deer mice after clearcutting, and resulting increase in seed predation, was hampering the regeneration of an endangered plant, *Trillium ovatum*. Similarly, the postfire increase in deer mice may slow down the rate of forest regeneration (Chapter 5). Moreover, red-backed voles are known to be the main dispersal vector for mycorrhizal fungi, which are crucial for the regeneration of coniferous trees (Maser et al. 1978). It is difficult to judge how these interactions may differ between areas subjected to wildfire and forest harvest because responses of small mammals to natural and anthropogenic disturbances differ only quantitatively, not qualitatively (i.e. by the magnitude of change, not by its direction).

### Conclusions

The results of this study demonstrate that the qualitative responses of small mammals to disturbance are species-specific, but relatively consistent across fires and different cutting regimes. However, the type of disturbance strongly influences the magnitude of that response. According to their effects on small mammals, disturbances can be ranked from mild (partial harvest), through moderate (clearcutting) to severe (stand-replacement wildfire). As found with other taxa, the effects of forest harvest on small mammals are not equivalent to those of wildfire. Still, the ecological consequences of these differences remain unknown and deserve future investigation.

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## CHAPTER 3

### DEER MOUSE DEMOGRAPHY IN BURNED AND UNBURNED FOREST: NO EVIDENCE FOR SOURCE-SINK DYNAMICS

Abstract: Deer mouse (*Peromyscus maniculatus*) populations increase dramatically after wildfire. These increases are puzzling because there are no obvious food sources or vegetation cover in severely burned areas. We conducted a capture-mark-recapture study of deer mice in a mosaic of burned and unburned montane forest in western Montana to determine if their postfire increase could be explained by source-sink dynamics, with burned areas acting as a sink. When overall mouse densities were very low, the vast majority of the population was found in burned areas. Mice appeared regularly in unburned forest only when the densities were high. This pattern is precisely opposite to the expected results if the sink hypothesis were correct. Moreover, mice in burned areas did not show decreased body weight, reproductive performance, or survival when compared to mice in unburned areas. Age structure and sex ratio did not differ between burned and unburned sites. We conclude that burned areas do not function as population sinks; rather, they represent high-quality habitat for deer mice.

## Introduction

Habitat quality is a central theme of spatial population ecology and wildlife management (e.g. Pulliam 1996; Rodenhouse et al. 1997; Root 1998; Franken and Hik 2004). Natural environments are patchy, and thus habitat quality changes across space. This patchiness is particularly pronounced after disturbances such as fire, which often results in sharp boundaries and drastic differences between affected and unaffected areas. Even though we expect that species with wide ecological tolerance will often occupy both disturbed and undisturbed patches, habitat quality is likely to be different. Similarly, we expect population dynamics to vary between disturbed and undisturbed patches.

Traditionally, ecologists assumed that all suitable habitat patches would be occupied and that a species would only occur in suitable habitat (Pulliam 1996). Habitat-specific demography was ignored and population density served as the primary measure of habitat quality (Van Horne 1983). This view has been challenged by the concept of a dispersal sink (Anderson 1970; Lidicker 1975). Dispersal sinks were usually thought to be of low quality, but in some situations sink populations could reach high densities (Lidicker 1975). Later, mechanistic source-sink models (Holt 1985; Pulliam 1988) quantified those circumstances when low-quality habitat would nevertheless be characterized by high population density. Source-sink models predict that fitness differs among habitats as a consequence of passive dispersal (Holt 1985), territorial interactions (Pulliam 1988; Pulliam and Danielson 1991) or maladaptive habitat choice (e.g. Delibes et al. 2001). The source-sink model quickly gained enormous popularity, but its prevalence in natural systems is unclear (see reviews by Diffendorfer 1998 and by Runge et al. 2006). Alternative models of population dynamics in heterogeneous environments predict that fitness will tend to equalize among habitats (e.g. Fretwell and Lucas 1970; McPeck and Holt 1992). The concept of ideal habitat selection (Fretwell and Lucas 1970; Morris et al. 2004) assumes that animals always choose the best habitat available and that habitat quality declines with the density of conspecifics. Thus, population density might differ among habitats with different carrying capacities, but the average fitness will not.

In the present study, we investigated demography and habitat selection of deer mice, *Peromyscus maniculatus*, in burned and unburned montane forest. This species is renowned for its capability for spectacular increase in abundance after forest disturbances

such as wild and prescribed fire (e.g. Halvorson 1982; Bock and Bock 1983; Martell 1984; Crête et al. 1995; Converse et al. 2006c). These increases are puzzling for several reasons. First, there is no apparent food in severely burned areas. Second, severe fire often removes all vegetation and even litter, thus mice appear to be at increased risk of predation. Moreover, several studies suggested that deer mice prefer microhabitats with dense vegetation cover (e.g. Bowers and Smith 1979; Morris 2005; Craig et al. 2006), and experimental studies have shown that mice in such areas suffer less predation than in open sites (Longland and Price 1991). Therefore the idea that severely burned sites function as sink habitats for deer mice is intuitively appealing. Such a solution to the apparent paradox of postfire increase in deer mice after severe wildfire has been suggested by Buech et al. (1977), Martell (1984), and subsequently repeated in a recent review by Fisher and Wilkinson (2005).

We examined two related hypotheses: (1) burned montane forest represents low-quality deer mouse habitat, and (2) the postfire increase in deer mice is a result of immigration from unburned sites rather than a consequence of intense *in situ* reproduction. To test the first hypothesis, we compared survival, body mass, and density in burned and unburned forest during times of high and low abundance. Survival has been recognized for a long time as an important determinant of habitat quality (Van Horne 1982) and more recently as a vital rate of high importance to population growth in the vast majority of investigated species (e.g. Pfister 1998; Crone 2001) including deer mice (Citta 1996). Adult body mass (a proximate measure of condition) should be lower in low quality habitats; dominant individuals inhabiting high suitability areas are expected to have higher body mass than subordinate individuals found in lower-quality habitat (e.g. Van Horne 1981; Halama and Dueser 1994). Finally, during times of low abundance, agonistic and territorial interactions in deer mice are rare (Wolff 1985; 1989) and mice are supposedly “free” to select their preferred habitat. Therefore, if burned areas serve as sinks, when deer mouse density is low most mice should be found in unburned areas.

To test the second hypothesis, immigration as a cause of population increase, we compared reproductive effort in burned and unburned areas. If the population increases in burned forest result from immigration rather than *in situ* reproduction, deer mouse

reproduction in burned areas would be markedly lower than in unburned areas. Additionally, we compared the age structure and sex ratio in burned and unburned areas. If dispersal is biased by age or sex, spatially variable age structure or sex ratios may be a sign of spatially imbalanced dispersal (Doncaster et al. 1997), possibly caused by source-sink dynamics (Gundersen et al. 2001).

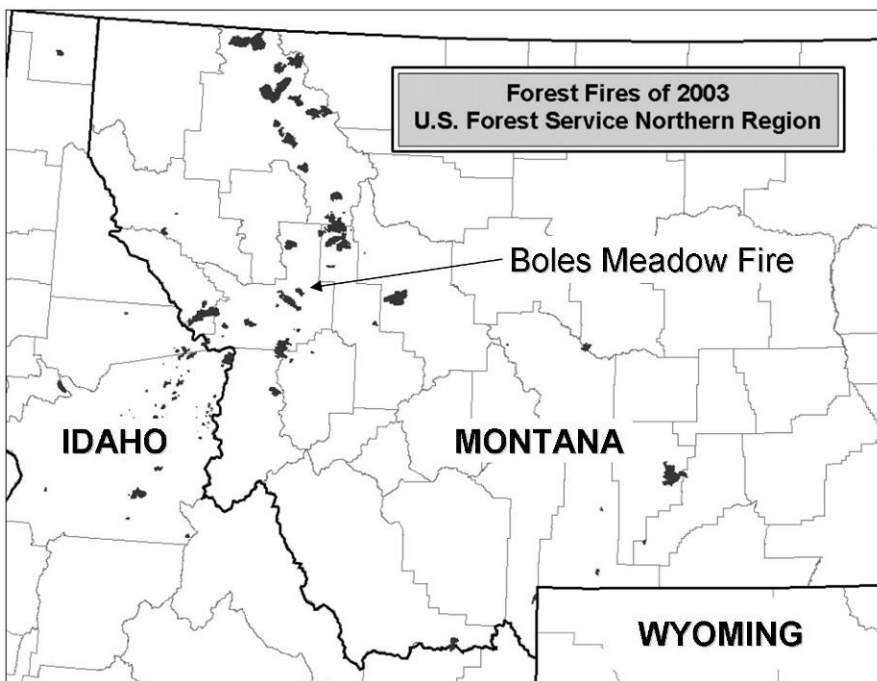
If the quality of burned areas is indeed low, it would be a spectacular example of “abundance as a misleading indicator of habitat quality” (Van Horne 1983; Pidgeon et al. 2003). Moreover, if movement from unburned areas caused the population increase, this could be a case of high-density sink population maintained by influx of surplus individuals from low-density source. This situation was envisioned by Pulliam (1988), but to our best knowledge has not been yet reported in empirical studies. On the other hand, if the quality of burned areas is high, this counterintuitive result would demonstrate that disturbances that seem very damaging may actually increase habitat quality for certain generalist species, even if they are usually associated with undisturbed habitat types (Foresman 2001).

## Materials and Methods

### Study Site

The study was conducted at Boles Meadow (47°60'N, 113 °45'W), located in the Seeley Valley, approximately 40 km northeast of Missoula, Montana, U.S.A (Fig. 1). The area was predominantly Douglas-fir (*Pseudotsuga menziensis*)/western larch (*Larix occidentalis*) forest. The understory was dominated by beargrass (*Xerophyllum tenax*) and huckleberry (*Vaccinium* sp.). Boles Meadow burned in August 2003 in a lightning strike-induced fire that encompassed 2000 ha of forest. At the beginning of summer 2004, six trapping grids were constructed: two (C1 and C2) in unburned and four (F1-F4) in burned forest. The design is unbalanced because the study was intended as an investigation into the effects of salvage logging on wildlife and sites F3 and F4 were supposed to be harvested, although logging did not occur until late summer 2005. All F-grids were located within a high-severity burn, where fire killed all trees and completely removed the litter layer. During the first year after fire, there was little to no understory vegetation in these trapping grids. In the second year after fire, the understory consisted

mainly of fireweed (*Epilobium angustifolium*) and heart-leaved Arnica, *Arnica cordifolia*) (Plate 1, see also Chapter 1 for more detailed description of the effects of fire on vegetation). With the exception of F4, which was on a north aspect, the trapping grids were located on southern aspects, at elevations ranging from 1721 to 1869 m. Median distance between grids equaled 2.2 km (maximum 5 km). All grids were located more than 200 m from the edge of the burn and, in the case of F-grids, from unburned patches within the burned area.



**Fig. 1.** Wildfires that burned in the area of western Montana in 2003 (source: National Resource Information System, <http://nris.mt.gov>, modified), with the study site indicated by an arrow.



**Plate 1.**—Montane forest at Boles Meadow, west-central Montana, one year (left) and two years (right) after stand-replacement fire. Photo credit R. Zwolak.

### Trapping Procedure

We used a robust design with four primary sessions, each consisting of four secondary sessions (Pollock 1982; Pollock et al. 1990). Trapping was conducted during summer 2004 and 2005. The interval between consecutive primary sessions was three weeks with secondary sessions consisting of four nights and days of trapping. This design should yield reliable estimates of survival and population density (Pollock 1982). Because daytime captures of deer mice were very uncommon, days rarely provided additional information; we pooled daytime and nighttime captures into 24-h periods. Concurrent trapping at all grids was unfeasible for logistic reasons; thus the sites were divided into two sets, each consisting of one unburned and two burned areas. Sites within each set were trapped at the same time. In 2004, trapping at sites C1, F1, and F3 began June 1 and ended August 6. At sites C2, F2, and F4 trapping began June 8 and ended August 13 in 2004. In 2005, the schedule was the same as in 2004, but trapping began



and ended one day sooner. Because of salvage logging, the fourth primary trapping session in 2005 could not be conducted at site F3.

In 2004, each of the six grids consisted of 100 trapping stations arranged in a 10 x 10 square with 10 m spacing between traps. To increase the number of captures and hence the precision of population estimates, in 2005 the grids were enlarged to 144 trap stations (12 x 12). One folding Sherman™ live trap was placed at each station. The traps were covered with foam sheets or open-ended waxed milk cartoons, supplied with polyester bedding, and baited with oats and a small piece of carrot. Each captured mouse was individually marked by toe clipping. We used the marking scheme proposed by Melchior and Iwen (1965), which enables to mark up to 899 numbers without clipping more than one toe per foot. All capture, handling, and marking procedures followed the guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998).

### Demographic Analyses

Deer mice captures were analyzed with program MARK (White and Burnham 1999) separately for years 2004 and 2005. We used Huggins closed robust design (Huggins 1989, 1991) because of its good performance given sparse data (Conn et al. 2006). The most parsimonious models were determined with Akaike's information criterion corrected for small sample size ( $AIC_c$ ) and ranked according to  $\Delta AIC_c$ . The model that fits data best receives  $\Delta AIC_c$  equal 0. Models with  $\Delta AIC_c \leq 2$  have strong support, those with  $4 \geq \Delta AIC_c \leq 7$  have considerably less support, and those with  $\Delta AIC_c > 10$  have basically no support (Burnham and Anderson 2002).  $\Delta AIC_c$  weights represent another convenient method of comparing the strength of evidence: they can be interpreted as the probability that a given model is the best for the data (Burnham and Anderson 2002).

Since between-site movement was extremely rare (five out of 241 individuals captured in 2004 and four out of 102 in 2005 moved among burned sites), each captured individual was assigned to a group according to the trapping site (six groups). Temporary emigration ( $\gamma$ ) was not frequent enough to be estimated and was set to 0 in all models. Apparent survival ( $\Phi$ , estimates presented for 21-d periods), capture ( $p$ ), and recapture ( $c$ )

probabilities were modeled as (1) constant, (2) differing between burned and unburned sites, (3) changing among primary periods, or (4) changing both between burned and unburned sites and among primary periods. Apparent survival, capture, and recapture were allowed to vary independently, thus there were  $4 \times 4 \times 4 = 64$  models for each year. Over-parameterized models (determined by the examination of standard errors of estimates and parameter counts) were removed from analysis. Estimates were model-averaged to reduce model selection bias (Burnham and Anderson 2002) and presented with unconditional standard errors (SE) or 95% confidence intervals (95% CI).

To derive estimates of deer mouse abundance in burned and unburned areas we averaged estimates from particular trapping sites. A variance estimate that explicitly incorporates sampling variation of individual sites was derived using the Delta method (Seber 1982:138):

$$[(\text{sum of the variances of site-specific mark-recapture estimates}) / n^2],$$

where  $n$  is the number of burned ( $n = 4$ ) or unburned ( $n = 2$ ) sites.

We calculated 95% CI of the abundance estimates using the following formula (Chao 1989):

$$M_{t+1} + \frac{f_0}{C}, M_{t+1} + f_0 C$$

$$\text{Where } C = \exp \left( 1.96 \sqrt{\log \left[ 1 + \frac{\text{var}(\hat{N})}{f_0^2} \right]} \right) \text{ and } f_0 = \hat{N} - M_{t+1} \text{ is the number of}$$

individuals not captured, and  $M_{t+1}$  is the number of unique animals captured.

To assess population density, we estimated sampling area as the grid area plus a boundary strip equal to mean maximum distance between the two farthest capture locations (“mean maximum distance moved” or “MMDM”):

$$\hat{A} = L^2 + 4L (\text{MMDM}) + \pi (\text{MMDM})$$

where  $\hat{A}$  = the estimated area of a grid and  $L$  is length of grid side (after Parmenter et al. 2003). The variance of  $\hat{A}$  was estimated with the Delta method (Parmenter et al. 2003):

$$\text{Var}(\hat{A}) = (4L + 2 \pi (\text{MMDM}))^2 \text{Var}(\text{MMDM}).$$

Mean minimum distance moved was calculated for each deer mouse captured at least twice in a given primary period (individuals fulfilling this condition in more than one primary period entered the analysis more than once). This approach compensates for the increase of the actual trapping area caused by captures of animals with home ranges only partially enclosed by grid. Although the theoretical assumptions of this method are controversial (Parmenter et al. 2003), it has performed well both in simulations (Wilson and Anderson 1985) and empirical studies (Parmenter et al. 2003).

### Reproduction

Reproductive effort was estimated by the percent of females and males captured in reproductively active condition in each primary period. Females were considered reproductively active when pregnant (visible nipples and distended belly) or lactating (enlarged nipples) and males when scrotal (descended testes). As the same individual could be reproductively active in one primary period and inactive in another, the reproductive status of the same individual in different primary periods was treated as a separate sample. For this index, both the number of mice and the duration of reproductive activity are of equal importance. Since mice can have more than one litter per season, a longer period of reproductive activity contributes to higher reproduction. Thus, metrics counting the proportion of reproductive mice in each primary sample period regardless of identity is useful, even though the samples are not strictly independent.

### Body Mass of Adult Mice

All deer mice were weighed with Pesola<sup>TM</sup> scales at their first capture in each primary period. Adult mice were defined as individuals that completed the post-subadult molt, as indicated by a brown pelt (juvenile pelt is grey). This molt is usually finished by the twenty-first week of age (Layne 1968). Even though some young of the year completed the post-subadult molt near the end of the summer, this class consisted mostly of overwintered individuals. If the same adult animal was captured in more than one primary period, its average mass was used for the comparison. To avoid bias, pregnant females were excluded from the analysis.

### Age Structure and Sex Ratio

Adults and juveniles were categorized according to their pelt as described above. Age structure was expressed as the proportion of juveniles among individuals captured in a given primary period. Sex ratio was expressed as the percentage of males or females among all individuals captured throughout the summer.

## Results

### Capture Rates and Probabilities

We captured and individually marked 241 (209 in burned and 32 in unburned areas) and 102 (94 in burned; 8 in unburned) deer mice in 2004 and 2005, respectively. The “best” models, according to  $AIC_c$  values, are presented in Table 1. In 2004, the highest-ranking models were those where survival varied over time and recapture probability differed between burned and unburned areas and changed over time. The results on capture probability were less conclusive (Table 1). In 2005, the best model constrained all variation in survival, capture and recapture probability, but small differences in  $AIC_c$  values indicate that there was no clear winner (Table 1). Model-averaged capture probabilities were very similar in burned and unburned areas and ranged from 0.26 (SE = 0.05) to 0.34 (SE = 0.05) (Table 2). In both years, mice demonstrated a strong “trap-happy” behavioral response, with estimated recapture probabilities being, on average, 2.45 times higher than capture probabilities in the same primary period and site category (i.e., burned or unburned, Table 2). There was no consistent difference in recapture probability between burned and unburned areas and there was no apparent increasing or decreasing trend throughout the summer.

**Table 1.** Top 10 models used to describe abundance and survival of deer mice in burned and unburned forest in year 2004 and 2005. Apparent survival ( $\Phi$ ), probability of capture ( $p$ ), and probability of recapture ( $c$ ) were modeled as constant ( $\cdot$ ), varying between burned and unburned sites (Fire), varying among primary periods (PP), and varying among primary periods and sites (PP\*Fire). The models were run in program MARK and evaluated by adjusted Akaike's information criteria,  $AIC_c$ .

2004					2005				
Model					Model				
$\Phi$	$p$	$c$	#P	$\Delta AIC_c$	$\Phi$	$p$	$c$	#P	$\Delta AIC_c$
PP	(.)	PP*Fire	12	0.000	(.)	(.)	(.)	3	0.000
PP	Fire	PP*Fire	13	2.090	(.)	(.)	Fire	4	0.579
PP	PP	PP*Fire	15	3.296	PP	(.)	(.)	5	0.914
PP*Fire	(.)	PP*Fire	15	4.945	Fire	(.)	(.)	4	0.950
(.)	(.)	PP*Fire	10	5.843	PP	(.)	Fire	6	1.518
PP*Fire	Fire	PP*Fire	16	6.898	Fire	(.)	Fire	5	1.541
Fire	(.)	PP*Fire	11	7.788	(.)	Fire	(.)	4	1.850
(.)	Fire	PP*Fire	11	7.878	(.)	(.)	PP	6	1.980
PP*Fire	PP	PP*Fire	18	8.353	(.)	Fire	Fire	5	2.441
(.)	PP	PP*Fire	13	8.735	PP	Fire	(.)	6	2.627

**Table 2.** Model-averaged probability of capture ( $p$ ) and recapture ( $c$ ) in each primary period (1-4) during summer 2004 and 2005. Unconditional standard error is given in parenthesis.

2004

Site Category	Probability of capture ( $p$ )				Probability of recapture ( $c$ )			
	1	2	3	4	1	2	3	4
Unburned	0.26 (0.05)	0.28 (0.05)	0.27 (0.04)	0.27 (0.04)	0.67 (0.14)	0.30 (0.10)	0.86 (0.07)	0.95 (0.05)
Burned	0.26 (0.05)	0.28 (0.05)	0.27 (0.04)	0.27 (0.04)	0.50 (0.07)	0.57 (0.05)	0.63 (0.04)	0.60 (0.04)

2005

Site Category	Probability of capture ( $p$ )				Probability of recapture ( $c$ )			
	1	2	3	4	1	2	3	4
Unburned	0.31 (0.11)	0.32 (0.10)	0.31 (0.08)	0.31 (0.08)	0.80 (0.08)	0.80 (0.08)	0.80 (0.08)	0.78 (0.08)
Burned	0.33 (0.05)	0.34 (0.05)	0.34 (0.04)	0.34 (0.04)	0.84 (0.03)	0.85 (0.03)	0.84 (0.03)	0.82 (0.03)

### MMDM and Effective Grid Size

Mean maximum distance moved (MMDM) tended to decline throughout the summer, but not significantly so (linear regression:  $F = 2.316$ , d.f. = 1, 201,  $P = 0.103$ , slope (SE) = -2.782 (1.828) for 2004 and  $F = 0.530$ , d.f. = 1, 113,  $P = 0.468$ , slope (SE) = -2.009 (2.760) for 2005). Therefore we did not vary effective grid sizes with trapping sessions. In 2004, the MMDM in unburned areas was estimated as 48.9 m (SE = 5.4 m), whereas that in burned areas as 36.3 m (SE = 1.9 m). This difference was significant ( $t = 2.225$ , d.f. = 215,  $P = 0.027$ ), hence we used different effective grid sizes for the burned (2.53 ha) and unburned (3.32 ha) areas. In 2005, the difference in MMDM between burned and unburned sites was non-significant ( $t = 1.024$ , d.f. = 97,  $P = 0.308$ ) and we used one value of MMDM, 44.5 m (SE = 2.8 m), to calculate the effective grid size, which equaled 3.79 ha.

### Population Density

Throughout the first summer after fire, densities of mice in unburned areas remained relatively low (approx. 2 mice per hectare), whereas those in burned areas increased markedly, despite having started at a similar level (Fig. 2). As a consequence of this increase, in the last trapping session in August, the average density of deer mice in burned areas was estimated as 14.0 mice/ha (95% CI: 12.7-16.7 mice/ha), over five times higher than the mean density in unburned sites at the same time (2.7 mice/ha, 95% CI: 2.3-3.8). In 2005, mouse density was markedly lower both in burned and unburned sites (Fig.2). However, the general pattern remained unchanged: deer mouse density in burned areas was 4.4 – 5.5 times higher than that in unburned areas. At the beginning of June, during the first trapping session, all captured mice were found in burned areas. In subsequent trapping sessions, mouse density increased both in burned and in unburned sites, but remained consistently lower in the latter (Fig. 2).

### Survival, Reproduction and Body Mass

In 2004, apparent survival was almost identical in burned and unburned areas, and tended to increase throughout the summer (Fig. 3). In 2005, due to low number of captures that year (particularly in unburned sites), survival estimates were characterized by large standard errors and the 95% CI overlap widely.

For both sexes and both years, the proportion of reproductively active deer mice was higher in burned areas (Table 3). However, due to the small number of adult individuals captured in unburned sites, none of the individual differences were statistically significant. When pooled across years and sexes, the reproductive activity was significantly higher in burned areas ( $\chi^2_{[1]} = 7.09, P = 0.008, n = 244$ ).

In 2004, the mean body mass of adult mice equaled 20.1 g (SE = 0.60 g) in unburned and 19.5 g (SE = 0.24) in burned areas. This difference was not significant ( $t = 0.944, \text{d.f.} = 99, P = 0.348$ ). Similarly, in 2005, the mean body mass in unburned (19.4 g, SE = 1.14 g) and burned areas (20.5 g, SE = 0.27 g) was not significantly different ( $t = 1.086, \text{d.f.} = 54, P = 0.282$ ).

#### Age Structure and Sex Ratio

In 2004, the proportion of juveniles increased throughout the summer, ranging from 0.28 in June to 0.67 in August, but did not differ between burned and unburned areas (Fisher's exact test,  $P > 0.5$  in each primary session). In 2005, the number of individuals captured in unburned areas was too small for statistical comparisons in all but the last primary period. Again, the difference in age structure was non-significant (Fisher's exact test,  $P > 0.99$ ).

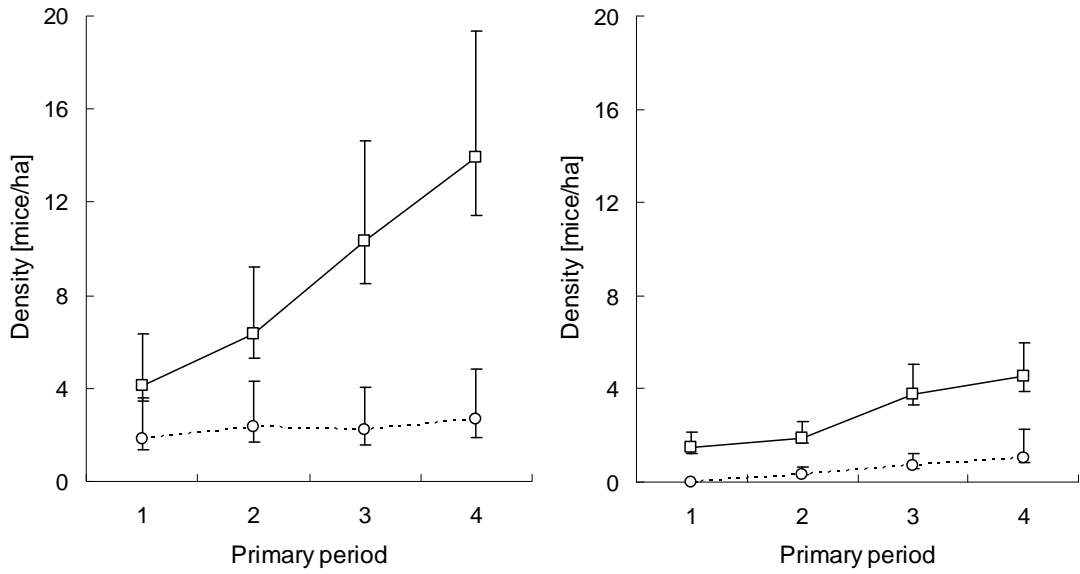
In 2004, the sex-ratio was female-biased, but did not differ between burned (60% females) and unburned (61% females) areas (Fisher's exact test,  $P > 0.99$ ). In 2005, more males than females were captured in both burned (67% males) and unburned (62% males) sites. The difference between burned and unburned areas was non-significant (Fisher's exact test,  $P > 0.99$ ).

**Table 3.** Percent of reproductively active deer mice in burned and unburned sites (sample size in parenthesis) and  $P$ -value for the difference (from Fisher's exact test).

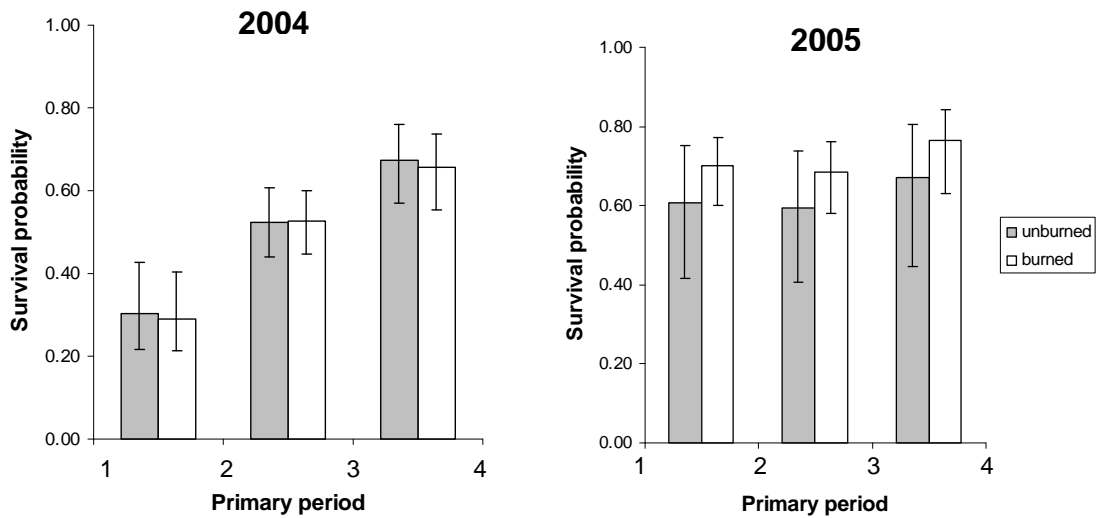
The sample consisted of individuals with body mass of at least 16 g.

Year	Sex	Burned sites	Unburned sites	$P$ -value
2004	Females	53% ( $n = 62$ )	40% ( $n = 15$ )	0.40
	Males	51% ( $n = 51$ )	20% ( $n = 10$ )	0.09
2005	Females	32% ( $n = 21$ )	0% ( $n = 1$ )	1.00
	Males	72% ( $n = 79$ )	40% ( $n = 5$ )	0.15





**Fig. 2.** Changes in the average density of mice in burned (solid line) and unburned forest (dotted line) during summer 2004 and 2005. The whiskers represent 95% CI of the estimates.



**Fig. 3.** Apparent survival (and SE) of deer mice in burned and unburned forest during summer 2004 and 2005. Estimates are model-averaged and presented for three-week periods between primary trapping sessions.

## Discussion

None of the measures used in this study indicates that the investigated burned areas served as population sinks or, more generally, represented low-quality deer mouse habitat. Our results suggest instead that (1) burned areas provide highly suitable habitat for deer mice, and (2) their postfire increase was mostly intrinsic. In 2004, densities in burned areas grew steadily throughout the summer, while those in unburned areas remained stable and relatively low. It could be argued that the unburned areas might function as sources, particularly because source populations are sometimes thought to be more stable than sink populations (Howe et al. 1991). However, if the burned areas were sinks, the drastic increase in deer mice would have to be caused by very intensive breeding in low-density unburned areas and subsequent migration into the burned areas. Moreover, if the burned areas were of low quality, reproduction in those sites should have been markedly lower or even absent. Our data demonstrated, instead, that reproduction in burned areas was similar or even higher than that in unburned areas. Therefore the increase in abundance in year 2004 was most likely intrinsic. Furthermore, high densities of deer mice were found in all the burned sites that we investigated, irrespective of their distance from the unburned forest. Although individual mice can disperse long distances, intense dispersal that influences population dynamics quickly attenuates with distance. The best (to our knowledge) study documenting the range of deer mouse dispersal capable of regulating population dynamics was conducted by Morris (1992) in Alberta badlands. He concluded that this distance does not exceed 140m.

At the beginning of summer 2005, mouse densities were very low. In this situation, territorial interactions should not interfere with habitat selection and, as predicted by the theory of habitat distribution (Fretwell and Lucas 1970), all or most individuals should be found in their preferred habitat. During that time, all (1<sup>st</sup> trapping session) or all but one (2<sup>nd</sup> trapping session) mice were found in burned areas. Mice were captured in unburned areas only after the densities in the burned areas increased. This finding agrees with the widely recognized pattern of decline in habitat selectiveness with increases in population density (Rosenzweig 1991).

The burned areas also seemed to represent high-quality overwintering habitat. During the first trapping session of 2005 (late May/early June), when patches of snow were still present, all mice were found in the burned areas. This may indicate that the

burned areas provide better chances of successful overwintering, or that mice choose to overwinter in burned areas, or both.

While our results refute the sink hypothesis, they closely match the theory of density-dependent habitat selection (Fretwell and Lucas 1970; Morris et al. 2004), which predicts that fitness will be equalized among habitats, whereas population density will be higher in habitats with greater carrying capacity. The low number of captures in unburned forest might have weakened our ability to detect habitat-specific differences in survival and reproduction. However, estimated parameters for survival and reproductive effort are similar or slightly higher in burned relative to unburned areas, which is consistent with density-dependent habitat selection, and highly inconsistent with source-sink dynamics.

Our study suggests that even a seemingly destructive disturbance may create high-quality habitat for a native species. However, why the burned areas are high quality is still a mystery and we encourage other researchers to investigate this phenomenon. One potential explanation is that fire actually enhances the availability of food resources for deer mice (Ahlgren 1966). For example, because severe fire burns the top soil layers, mice may have been able to access previously unexposed parts of the seed bank. To the best of our knowledge, this explanation has never been directly addressed and represents the next logical step in studying the postfire increase of deer mice. We are currently investigating this question in a different wildfire that occurred in 2005; our observations do not indicate increases in food sources such as insects and seeds (Chapter 4).

Causes other than food resources may also contribute to the increase of deer mice after wildfire and other disturbances. It is conceivable that mice in strongly disturbed areas experience predator release. Lack of vegetation cover greatly increases hunting success of owls (and probably other predators) preying on deer mice (Longland and Price 1991), but this effect could be counterbalanced by the decrease in predators in burned areas. Little is known about the abundance of predators after disturbances in North American conifer forests (Fisher and Wilkinson 2005), but similar estimates of mouse survival in burned and unburned areas do not indicate that these habitats differ in predation pressure.

Several studies (e.g. Hayes and Cross 1987; Graves et al. 1988; Carey and Johnson 1995, but see Barry 1990; Bowman et al. 2000) suggested that deer mice are associated with coarse woody debris (CWD), used for predation cover and travel.

Although CWD levels tended to be higher in burned than in unburned areas (see Chapter 1), there was no relationship between CWD volume and deer mouse abundance at a given trapping grid.

Furthermore, fire may reduce interspecific competition because species such as red-backed voles (*Myodes gapperi*) that are numerically dominant in undisturbed forest disappear after fire (e.g. Chapter 1). The existence of competition between deer mice and red-backed voles (e.g. Morris 1983; Wolff and Dueser 1986; Morris 1996; Schulte-Hostedde and Brooks 1997) and the importance of competition in structuring small mammal communities is controversial (e.g. Galindo and Krebs 1985). Therefore, this hypothesis is possible but not well supported by other studies at present time. Finally, the increase in deer mice occurs after wildfires in different types of coniferous and mixed forests and in different geographical areas (Krefting and Ahlgren 1974; Roppe and Hein 1978; Clough 1987; Crête et al. 1995; Kyle and Block 2000; Côte et al. 2003, but see Buech et al. 1977). Thus, it is possible that causes of the increase or their relative importance may differ among ecosystems.

The burned areas in our study provided high-quality habitat for deer mice. When overall mouse densities were very low (i.e. June and July 2005), the vast majority of the population was found in burned areas. Only when the densities were higher did mice appear in unburned forest. Thus, this pattern is precisely opposite from what we would expect if burned forests acted as population sinks. Moreover, the postfire increase in abundance seemed to be mostly intrinsic, as the reproductive rate in burned forest was at least as great as that exhibited by low-density populations in the unburned sites. Thus, in this particular case, abundance of deer mice is a valid indicator of habitat quality, further supporting the idea that there is unique ecological value in severely burned forests which needs to be weighed against the prevailing view that such natural disturbance events are “catastrophic” (DellaSala et al. 2006).

#### Acknowledgements

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## CHAPTER 4

### TWICE THE MICE:

#### WHY DO DEER MICE INCREASE IN ABUNDANCE AFTER FOREST FIRES?

Abstract: After stand replacing wildfires, deer mouse (*Peromyscus maniculatus*) abundance typically increases 2-5 fold, yet the cause of this increase remains unknown. We investigated four possible causes of postfire increase in deer mouse abundance, based on factors known to regulate populations: (1) increases in food resources (seeds and/or insects), (2) increased foraging efficiency of deer mice in burned, structurally simplified habitats, (3) decreased predation, and (4) source-sink dynamics, with burned forest acting as high-abundance sink. In burned vs. unburned forest, there were fewer seeds in soil core samples and similar abundance of ground-dwelling arthropods in pitfall traps. Thus, there were no obvious increases in food resources. In both burned and unburned forest, deer mice were captured more often in open microhabitats, and in foraging experiments, odds of insect and seed removal increased with increasing open area in one of two monthly trials. Thus, there was some evidence that mice may experience higher foraging success associated with reduced cover in burned areas. Deer mouse survival did not differ between burned and unburned forest, providing little support for the reduced predation hypothesis. Finally, similar survival and considerably higher reproduction in burned vs. unburned areas argues against the source-sink hypothesis. However, the fact that reproduction was higher in burned areas despite comparable or lower resource abundance suggests that the increase in deer mouse foraging success may have improved reproduction, despite being temporally variable. Thus, of the hypotheses we tested, the best explanation for the commonly observed increase in deer mouse populations following wildfire was an increase in foraging efficiency.

## Introduction

Disturbances strongly influence vertebrate populations (e.g. Karr and Freemark 1985, Whelan 1995, Pilliod et al. 2003, Fisher and Wilkinson 2005, Chapter 2 of this dissertation). This influence is usually mediated through profound changes in habitat structure and resource availability caused by disturbance (Whelan 1995). Still, while numerous studies have investigated how disturbances influence the abundance of wildlife, the specific causes of the impacts on vertebrates often remain unknown. Such information would be useful in predicting and possibly modifying the effects of natural and anthropogenic disturbances on wildlife. Moreover, determining habitat attributes that are affected after a disturbance and, in turn, trigger changes in vertebrate populations could improve our understanding of species-specific ecological requirements and factors that determine habitat quality.

In the western portion of North America, fire is among the most important ecological disturbances (Agee 1993). Deer mice (*Peromyscus maniculatus*), widespread and common generalist rodents, increase in abundance after forest fires (synthesis in Chapter 2). This increase may have important ecological consequences (Chapter 5), but its specific causes remain unknown. Increases in deer mouse populations are most often hypothesized to reflect an increase in food resources (either insects or seeds; Ahlgren 1966, Krefting and Ahlgren 1974, Nappi et al. 2004, Larsen et al. 2007). However, food availability is also a function of foraging success, which may be higher in burned forest due to simplification of habitat structure, as suggested by experiments conducted in grasslands (Reed et al. 2004, 2005). Predation is another factor known to regulate rodent populations (Hanski et al. 2001). Thus, post-fire population increases could reflect declines in predation, in relation to fire-induced changes in habitat structure or predator abundance. All the above explanations imply improvements in habitat quality following fire. Alternatively, forest fires could reduce the quality of deer mouse habitat (e.g., via reduced food availability or increased predation), thereby creating population sinks filled by surplus individuals from unburned forest (Buech 1977, Martell 1984, Fisher and Wilkinson 2005).

With the exception of the last hypothesis, tested and rejected by Zwolak and Foresman 2008 (Chapter 3), these explanations have not been critically evaluated, individually or collectively. We investigated deer mouse populations in recently burned and unburned montane forest and collected observational and experimental data on the availability of food resources, microhabitat selection, and deer mouse

demography to assess these possible explanations for postfire increases in deer mouse abundance. Below, we outline these hypotheses more specifically, including associated predictions.

#### Hypotheses and predictions

*Hypothesis 1: Increased food resources.* Although deer mice eat a variety of food items, arthropods and seed consistently dominate their diet (Martell and Macaulay 1981, Wolff et al. 1985, Pearson et al. 2000). Thus, if the postfire increase in deer mice results from the high abundance of food resources in burned forest, we expected that burned sites would have more seeds and/or arthropods, particularly of taxa commonly consumed by deer mice, e.g., Coleoptera, Orthoptera, or Arachnida (D. Pearson, *unpublished data*), relative to unburned forest. In addition, if more food were available, changes in deer mouse abundance would likely be caused by increased reproduction in burned stands. Experimental food additions (Schweiger and Boutin 1995, Galindo-Leal and Krebs 1998, Banks and Dickman 2000, Diaz and Alfonso 2003) and studies on rodent responses to natural food pulses (Pucek et al. 1993, Marcello et al. 2008, but see Fitzgerald et al. 2004) demonstrate that increased food availability often triggers an increase in rodent reproductive activity.

*Hypothesis 2: Increased foraging success.* 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). Pearson et al. (2001) showed that deer mice select open microhabitats even in relative sparse vegetation types and hypothesized this was due to increased foraging efficiency in areas of reduced vegetative cover. If the postfire simplification of habitat structure makes mouse foraging more efficient, we expected that deer mice would be more active (and therefore captured more often) in open as opposed to densely vegetated microhabitats, and that in foraging experiments, mice will remove more food items from open than from densely vegetated microhabitats. As with increased food resources (hypothesis 1), increased foraging success would most likely lead to higher abundance through increased reproduction.

*Hypothesis 3: Reduced predation.* If reduced predation was responsible for increased post-fire abundance of mice, higher abundances would almost certainly be caused by higher survival of mice in burned than unburned forest. Predation strongly affects rodent habitat selection (Kotler and Brown 1988). In particular, rodents avoid open areas in habitats if the risk of predation is high (Longland and Price 1991,

Dickman 1992, Lagos et al. 1995). Therefore, if reduced predatory pressure was responsible for post-fire increases in mice, we expected that deer mice would exhibit stronger preference (or weaker avoidance) of open habitats in burned vs. unburned forest.

*Hypothesis 4: Source-sink dynamics.* Increased deer mouse abundance could be caused by movement of mice from unburned forest (presumably high-quality habitat) into burned forest (presumably low-quality: Van Horne 1983; see extended discussion in Zwolak and Foresman 2008). If this were the cause of increased mouse densities, we expected that survival and/or fecundity of mice would be higher in unburned forest. Patterns of mouse population size in a very similar system were inconsistent with this mechanism (Zwolak and Foresman 2008), but here we revisit this question in the context of these alternative hypotheses.

## Materials and Methods

### Study Site

We conducted this study in west-central Montana, U.S.A., within and nearby the area burned in 2005 by the I-90 wildfire, approximately 50 km west of Missoula, MT. We selected six study stands, three that were burned with a stand-replacement fire and three in adjacent unburned forest. The forest was dominated by Douglas-fir (*Pseudotsuga menziesii*), with western larch (*Larix occidentalis*), lodgepole pine (*Pinus contorta*), and ponderosa pine (*Pinus ponderosa*). The selected stands were west or south-facing, located at elevations ranging from 1600 to 1900 m, and at least 0.85 km from one another.

### Live Trapping

We trapped mice during summers 2006 and 2007 in monthly sessions (June-July-August), each consisting of 4 consecutive trap-nights (the only exception was the August 2007 trapping session at the last pair of sites, which was ended after 3 nights due to adverse weather). At each study site, we set out 169 Sherman live traps in a 13 by 13 grid with 10 m trap spacing. The traps were baited with oats and supplied with polyester bedding. We opened the traps at 6:00-7:00 pm and closed them by 10:00 am. We marked each captured rodent with a uniquely numbered eartag, and recorded its weight 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 unharmed. Our research followed ASM guidelines (Gannon et al. 2007) and was approved by the University of Montana Institutional Animal Care and Use Committee.

#### The availability of food resources: seed and insect sampling

To assess food availability, we measured arthropod abundance and sampled the seed bank in burned and unburned forest. Soil seed bank samples were taken in June and August 2006 and 2007. Each time, we collected soil cores from 12 randomly selected points within each trapping grid using a standard 5 cm x 15 cm bulb planter. The samples were sifted and seeds counted and visually 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 preservative. Pitfall traps were left open for two weeks in July 2006 and 2007 and checked weekly. We identified collected arthropods to order, measured body length to the nearest 0.01 mm.

#### Microhabitat

We visually estimated ground cover (%) of microhabitat variables in 2-m radius circles centered at trap stations within each grid (169 circles/grid) to allow assessment of microhabitat selection by deer mice. The surveys were conducted in July 2006 and 2007. 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. In each circle, we counted saplings (height less than 2.5 m) and trees (height over 2.5 m), with trees divided in three diameter classes: small (diameter at breast height [DBH] <10 cm), medium (10 cm ≤ DBH ≤ 30 cm), and large (DBH > 30 cm).

#### Foraging Experiments

To assess foraging success, 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 stands per night. The insects (commercially available crickets, *Gryllus bimaculatus*) were attached with 0.2 mm filaments (50 cm length) looped around their necks and tied to wire flags marking trapping stations (Plate 1; Belovsky et al. 1990, Hedrick and Kortet 2006). For these

trials, we used every second trap station; thus the tethered insects were spaced 20 m from each other. At the 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 in the morning. Missing crickets were considered predated. In most such cases, the line was cut, presumably by the predator, and in some instances we discovered uneaten remains of tethered crickets (usually heads).

Conifer seeds were set out and examined at the same time as insects, but at alternate trapping stations. At each selected station, two seeds (one ponderosa pine and one Douglas-fir) were left on the 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.



**Plate 1.**—Foraging experiment: cricket (*Gryllus bimaculatus*) tethered to a wire flag in burned forest. Photo credit L. A. Reynolds.

#### Statistical analysis

Abundance and survival of deer mice were estimated with Program Mark (White and Burnham 1999) using Huggins closed robust design models (Huggins 1989, 1991), following the approach described in Zwolak and Foresman 2008. The

competing models, ranked according to their  $\Delta AIC_c$  values (lower values indicate higher likelihood of a model given the data), are presented in Appendix B. The effective sampling area of trapping grids (estimated with mean maximum distance moved: White et al. 1982) did not differ between burned and unburned forest.

The remaining statistical analyses were conducted in R (R Development Core Team 2005), using mixed effects models (function “lmer”). In each analysis, we included *trapping grid* ( $n = 6$ ) as random effects, whereas *fire* (“yes” for burned forest and “no” for unburned forest) and *year* (2006 or 2007) were entered as fixed effects. Other explanatory variables were specific to a given analysis and are described below. The best predictors were identified through backward stepwise elimination of non-significant ( $P > 0.05$ ) terms.

Number of insects (in pitfall traps) and seeds (in soil cores) were modeled using a Poisson distribution, or if data were over-dispersed, a quasi-Poisson distribution. In the later case, we used Markov chain Monte Carlo sampling (function “pvals.fnc”) to obtain *P*-values.

To examine microhabitat selection by deer mice we divided trap stations into those with and without captures in July (when we also sampled microhabitat variables), and conducted logistic regression, beginning with the global model that included microhabitat variables: percent cover *open area*, percent cover *coarse woody debris*, percent cover of *shrubs*, numbers of *saplings* and *trees*. We did not include % cover of *vegetation* because it was highly correlated with *open areas* ( $R = -0.84$ ).

Foraging experiments were analyzed with logistic regression, comparing stations where food was removed (predation event) or not removed. Fixed effects included percent of *open area* at a given trap station, *month* of the experiment (June or July), 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.

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, whereas *individual* (unique mouse) was included as a random effect.

## Results

### Mouse abundance

Deer mice accounted for 71% of all individuals captured during the study (Table 1). Other common species included chipmunks (*Tamias ruficaudus* and *T. amoenus*: not distinguished in this study), red-backed voles (*Myodes gapperi*) and shrews (*Sorex* spp.) On average, deer mice were estimated to be almost twice as abundant in burned than in unburned forest (1.6 times in 2006 and 1.8 times more abundant in 2007). However, there was considerable variation in the abundance estimates among time periods and stands (Table 2). In particular, one unburned stand had mouse abundances similar to the burned sites, whereas in the other two unburned stands, mouse abundances were markedly lower.

### Availability of seeds and insects

Soils samples collected in unburned forest contained on average  $2.03 \pm 0.18$  (SE) seeds whereas those in burned forest had only  $0.04 \pm 0.02$  (SE) seed per sample ( $z = -6.47$ ,  $P < 0.0001$ ). Douglas-fir represented 89% and 100% of seeds collected in unburned and burned forest, respectively.

The overall abundance of arthropods and the abundance of coleopterans did not differ between burned and unburned forest ( $P > 0.1$  in both 2006 and 2007, Fig. 1), whereas that of Arachnida was consistently lower in burned forest (2006:  $z = -9.63$ ,  $P < 0.0001$ , 2007:  $z = -4.33$ ,  $P < 0.0001$ , Fig. 1). In the first year after fire, the abundance 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. 1). The average length of arthropods did not differ between burned and unburned forest ( $t = -0.142$ ,  $P = 0.89$ ).

### Microhabitat selection

Deer mouse capture probability increased with the amount of open area and coarse woody debris (open area: odds ratio = 1.009 per % cover,  $z = 3.61$ ,  $P = 0.0003$ ; coarse woody debris: odds ratio = 1.031 per % cover,  $z = 3.93$ ,  $P < 0.0001$ ). This pattern did not differ between burned and unburned forest. In unburned forest, deer

mice were also more likely to be captured in areas with higher shrub cover, but this tendency was only marginally significant (odds ratio = 1.008,  $z = 1.88$ ,  $P = 0.059$ ). In burned forest where shrubs were rare (Fig. 2), their presence did not influence the probability of deer mouse capture ( $z = -1.57$ ,  $P = 0.117$ ). Not surprisingly, the probability of capture per station was strongly influenced by the abundance of deer mice at a given site ( $z = 10.32$ ,  $P < 0.0001$ ).

Considering those variables that influenced deer mouse microhabitat selection, burned forest had considerably more open areas (2006:  $t = 4.98$ ,  $P < 0.0001$ , 2007:  $t = 2.58$ ,  $P = 0.01$ , Fig. 2) and less shrub cover than unburned sites (2006:  $t = -2.90$ ,  $P = 0.004$ , 2007:  $t = -2.73$ ,  $P = 0.006$ , Fig. 2), whereas the amount of coarse woody debris did not differ between burned and unburned forest ( $P > 0.1$ , Fig. 2).

### Foraging experiments

Fewer insects were depredated in June than in July (40% vs. 63%,  $z = 3.71$ ,  $P = 0.0002$ ). Insects were more likely to be removed from open areas, with odds of attack increasing 1.020 times with every additional percent open area ( $z = 2.22$ ,  $P = 0.03$ ), but this effect occurred only in June trials. Insect removal rates did not differ between burned and unburned forest ( $P > 0.1$ ), thus the *fire* variable was not included in the final model.

Similarly, significantly more seeds were removed in the second month of the experiment, although this difference was very small (37% vs. 38%,  $z = 2.84$ ,  $P = 0.005$ ). The probability of seed removal marginally increased with the increase in percent open area (odds ratio = 1.014,  $z = 831$ ,  $P = 0.07$ ), but this effect occurred only in June trials in unburned forest. 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.

**Table 1.**—Individual small mammals captured in 2006 and 2007 in burned (F1-F3) and unburned (C1-C3) study sites.

**2006**

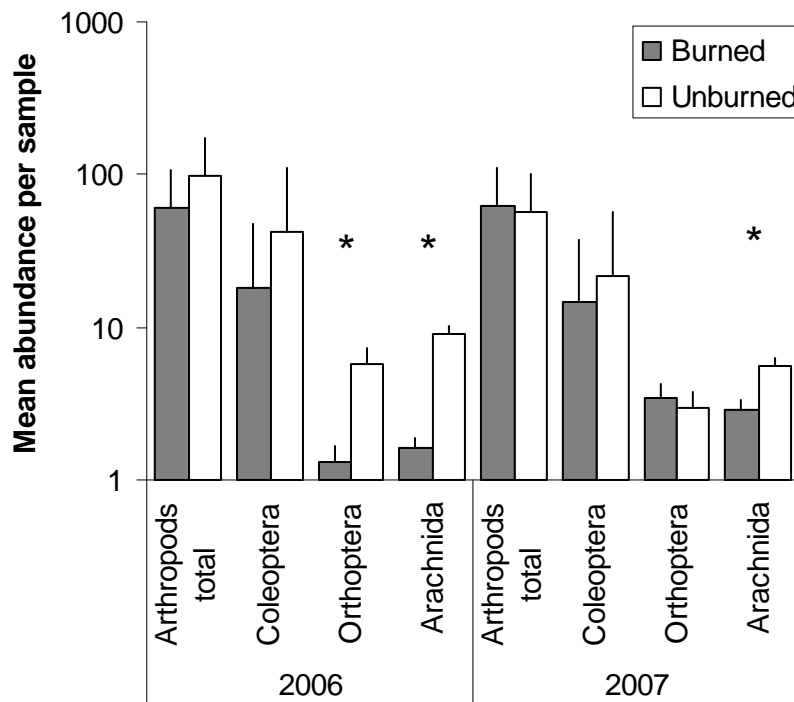
Site	<i>Peromyscus maniculatus</i>	<i>Tamias</i> spp.	<i>Myodes gapperi</i>	<i>Sorex</i> spp.	Other species
F1	24	5	0	0	0
F2	51	0	1	0	0
F3	54	2	0	0	0
C1	46	4	2	1	2
C2	14	10	23	21	0
C3	27	15	0	2	4

**2007**

Site	<i>Peromyscus maniculatus</i>	<i>Tamias</i> spp.	<i>Myodes gapperi</i>	<i>Sorex</i> spp.	Other species
F1	63	15	0	0	2
F2	131	12	0	0	8
F3	76	26	0	0	0
C1	57	7	1	1	0
C2	19	11	16	24	1
C3	46	29	0	5	1

**Table 2.**—Monthly estimates of deer mouse abundance in burned (F1-F3) and unburned (C1-C3) sites and associated unconditional standard errors. The estimates were derived from program “MARK”, using Huggins-type robust design models

Site	2006			2007		
	June	July	August	June	July	August
F1	18.4 ± 2.0	10.3 ± 1.9	13.5 ± 2.0	55.5 ± 13.9	40.7 ± 3.6	29.7 ± 2.4
F2	15.4 ± 2.0	23.5 ± 2.8	44.9 ± 4.5	49.8 ± 13.5	70.6 ± 5.0	107.4 ± 6.1
F3	20.0 ± 2.7	26.9 ± 3.4	30.3 ± 3.2	45.4 ± 12.1	44.9 ± 3.7	44.0 ± 4.3
C1	10.6 ± 1.5	26.8 ± 3.1	31.3 ± 3.3	50.6 ± 15.3	39.3 ± 3.5	33.3 ± 2.7
C2	3.4 ± 0.8	2.2 ± 0.6	11.4 ± 1.4	8.3 ± 3.3	9.8 ± 1.6	16.1 ± 1.7
C3	9.6 ± 1.5	14.9 ± 2.2	18.5 ± 2.4	57.7 ± 18.0	36.8 ± 3.4	14.0 ± 2.2

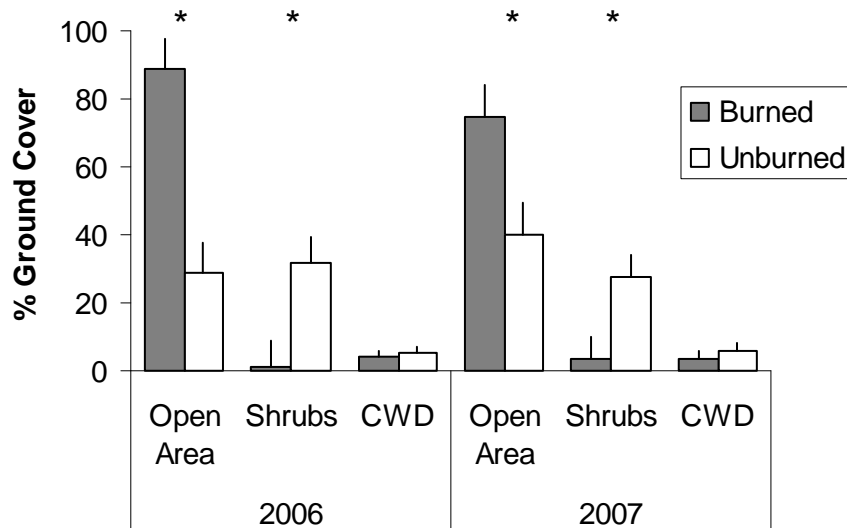


**Fig. 1.**—Abundance of arthropods captured in pitfall traps in burned and unburned forest. Bars denote standard errors and significant differences are marked with a star.

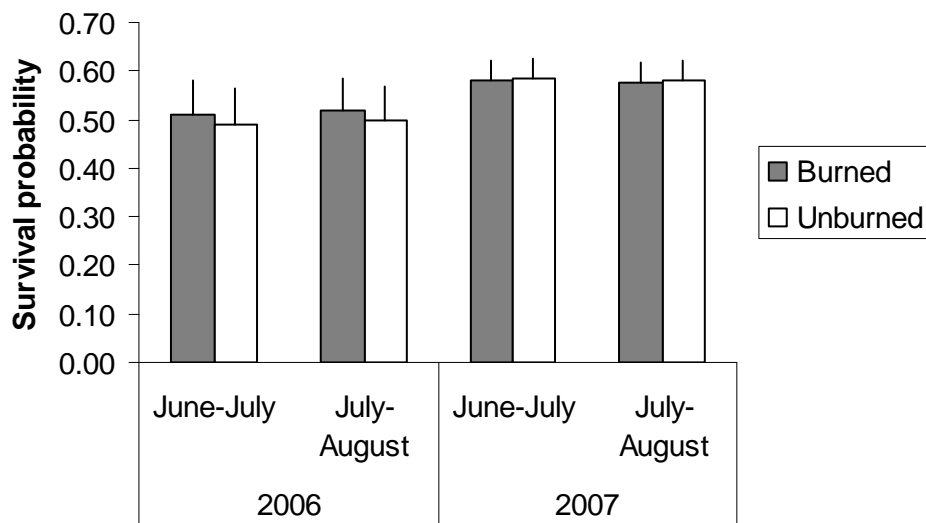
### Survival and reproduction of deer mice in burned vs. unburned forest

Model-averaged estimates of monthly apparent survival were nearly identical in burned and unburned forest, with widely overlapping standard errors (Fig. 3). However, reproductive activity differed considerably between burned and unburned forest. For males, after accounting for the significant effect of year (reproduction was more intense in 2006 than in 2007) and month (the proportion of reproductively active individuals 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,  $z = 3.35$ ,  $P = 0.001$ ). In the case of females, fire was the only significant predictor, with reproduction more intense in burned than in unburned forest (67% vs. 39%, 167 individuals, 250 observations,  $z = 4.05$ ,  $P < 0.0001$ ).





**Fig. 2.**—The average amount of open areas, shrubs, and coarse woody debris (CWD) expressed as percentage ground cover, in burned and unburned study sites. Bars denote standard errors; stars denote statistically significant differences.



**Fig. 3.**—Model-averaged estimates of apparent monthly survival in burned and unburned forest, derived from program “MARK”. Bars denote unconditional standard errors.

## Discussion

Deer mice were almost twice as abundant in burned than in unburned forest. This difference is consistent with widely occurring pattern of high postfire abundance of deer mice (Chapter 2), although it is moderate compared to some other studies (e.g., Krefting and Ahlgren 1974, Zwolak and Foresman 2008). In fact, this moderate average increase reflects substantial heterogeneity among reference sites. Two unburned stands had only one-third to one-fifth the abundance of burned sites, but the abundance of deer mice in the most open and xeric unburned site was similar to that in burned trapping grids (site C1 in Table 2).

The most commonly invoked explanation of postfire increase in deer mouse abundance, greater food resources in burned areas, was not supported by our data. There were considerably fewer seeds and similar overall abundance of arthropods in burned versus unburned forest. Moreover, invertebrate groups known to be common in deer mouse diets tended to be more abundant in unburned forest. This pattern does not rule out obscure changes in some unmeasured food source; however, we are not aware of any studies that document dramatic increases in deer mouse fecundity in response to changes in food resources other than seeds and arthropods.

The second hypothesis we tested is that fire-related simplification of habitat structure improves the foraging success of deer mice, even though we documented more food in burned areas. Consistent with this hypothesis, mice were captured more often in open than in closed microhabitats. Moreover, C1, the unburned site with high deer mouse abundance, was characterized by the highest amount of open areas among unburned trapping grids (C1: 54%, C2: 15%, C3: 36%), but did not exceed them in remaining variables that could potentially influence deer mice abundance (e.g. coarse woody debris or the abundance of insects). Finally, in foraging experiments, the odds of insect predation increased with % open area and there was a similar although non-significant trend toward higher seed removal. Still, these patterns occurred in only one of two monthly trials. Thus, there was inconclusive support for the increased foraging success hypothesis.

The third investigated hypothesis, reduced predation in burned areas, was not supported by our survival or habitat use results. There was no difference in deer mouse survival in burned and unburned forest. Therefore, if predation were affecting mouse abundance, it would have to do so via an obscure path through which reduced predation risk altered habitat use and subsequent fecundity, without directly affecting

survival. In fact, deer mouse preference for open areas and coarse woody debris did not differ between burned and unburned forest. There was weak preference for shrub cover in unburned, but not in burned forest. However, the lack of response of deer mice to shrub cover in burned forest was not surprising given the low availability in this vegetation type in burned trapping grids. Therefore, it seems unlikely that deer mice substantially changed habitat use in response to predation risk.

Finally, similar survival along with considerably higher reproductive activity of deer mice in burned forest, argue strongly against the source-sink hypothesis. These results are consistent with those reported by Zwolak and Foresman (2008) for an analysis of source-sink dynamics following a wildfire in wetter forest types.

In addition to the hypotheses we tested, some researchers have suggested that changes in mouse abundance may reflect changes in other species interactions, particularly interspecific competition or disease. It could be argued that the postfire increase in deer mice could be caused by the disappearance of red-backed voles from burned forest (Halvorson 1982, see Table 1). However, this relationship was most likely caused by the well-known differences in habitat preferences of these two species: red-backed voles are most abundant in mesic, and deer mice in xeric habitats (e.g. Morris 1996). While early studies suggested that red-backed voles dominate deer mice behaviorally (Crowell and Pimm 1976), later research often failed to find evidence of competition between these two species (Morris 1983, Wolff and Dueser 1986, Morris 1996, but see Schulte-Hostedde and Brooks 1997). Shrews are also greatly reduced by fire (Zwolak and Foresman 2007, this study), but the evidence of competition between shrews and mice is even more scant. The reduction of the entire small mammal assemblage in burned areas might have positive influence on deer mouse population growth (Merritt et al. 2001). However, it is difficult to think of plausible pathways by which changes in small mammal communities could increase deer mouse abundance without changing survival (as expected from antagonistic interactions) or food availability.

In the past year, a number of studies have shown strong effects of parasites on *Peromyscus* population dynamics (Pedersen et al. 2008, Vandegrift et al. 2008). Notably, these effects are often mediated through higher reproductive activity in unparasitized mice (Burns et al. 2005, Vandegrift et al. 2008). There is some evidence that wildfires reduce parasite infestation in birds and mammals (reviewed in Bendell 1974), suggesting the possibility that that deer mice in recently burned areas are less

exposed to parasites and therefore reproduce more intensely. To our knowledge there are no data to evaluate this explanation, and it could be a valuable avenue for future research.

Changes in rodent abundance are usually explained by shifts in predatory pressure (influencing survival) and food resources (acting on reproduction). While the survival of deer mice does not differ between burned and unburned forest, mice reproduce more intensely in burned stands. We did not find an obvious increase in food resources in burned forest, but there was some support for the hypothesis that deer mouse foraging success is higher in burned stands. The improved foraging efficiency could translate into higher reproductive activity (Schweiger and Boutin 1995, Galindo-Leal and Krebs 1998, Banks and Dickman 2000, Diaz and Alfonso 2003), potentially explaining the increased abundance of deer mice in burned stands. Alternatively, this increase could be caused by changes in parasites, which have recently been linked to mouse fecundity (Vandegrift et al. 2008). In both cases, however, it seems highly unlikely that changes in deer mouse abundance reflect simple trophic interactions. Instead, behavioral changes or changes in parasite communities related seem to drive dramatic changes in mouse abundance in response to disturbance.

### **Acknowledgements**

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CHAPTER 5  
SEED PREDATION BY DEER MICE  
REDUCES CONIFER RECRUITMENT IN BURNED MONTANE FOREST

Abstract: The effects of wildfire on forest dynamics are typically explained by examining effects of abiotic factors on plant performance and competition. Here, we demonstrate that vertebrates may mediate the effects of wildfire on conifer recruitment. We investigated seed predation by the deer mouse (*Peromyscus maniculatus*) and its effects on the emergence and establishment of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) seedlings in unburned and recently burned forest in west-central Montana, USA. Deer mice were almost two times more abundant in burned than in unburned stands. In seed offering experiments, overnight seed removal associated with deer mice was more intense in burned than in unburned forest. Ponderosa pine seeds were removed at higher rates than the smaller Douglas-fir seeds were. In seed addition experiments, emergence of seedlings in deer mouse-exclusion cages was low in unburned forest, but 5-9 times higher in burned forest. The overall emergence was lower for ponderosa pine versus Douglas-fir. Seedling survival to establishment was also considerably higher in burned than in unburned forest. However, in adjacent cages accessed by deer mice, emergence and establishment was extremely rare for both conifers in burned and unburned forest. Wildfire creates favorable conditions for seedling recruitment but seed predation by deer mice removes this advantage.

## Introduction

Wildfires are among the most important factors determining distribution, structure, and dynamics of plant communities worldwide (Whelan 1995, Bond et al. 2005). In western North America, the influence of recurring wildfires on tree communities is a focus of intense research (e.g. Kulakowski et al. 2004, MacKenzie et al. 2004, Brown and Wu 2005, Franklin et al. 2006, Keyser et al. 2008). Nonetheless, the majority of studies that investigate the effects of this disturbance on plant communities implicitly assume “bottom-up” control (reviewed in Whelan 1995, Agee 1993, Brown and Smith 2000, Rood et al. 2000, Buhk et al. 2007). In other words, changes in plant communities following wildfire are typically explained by direct effects of the physical environment on plant performance and competition, ignoring how vertebrates may mediate bottom-up effects.

Seed predation is recognized as one of the strongest forms of plant-animal interactions (Kelly and Sork 2002, Kolb et al. 2007). In North America, size-dependent seed predation by rodents has been demonstrated to control the transition between desert and grassland in the southern United States (Brown and Heske 1990); in northeastern hardwoods, seed predation greatly influences the rate and species composition of tree invasion in old fields (Ostfeld et al. 1997). However, in coniferous forests of western North America, wildfire is believed to drive vegetation patterns (Agee 1993), and researchers have primarily studied rodents in the context of their response to disturbances, including wildfire (Stout et al. 1971, Roppe and Hein 1978, Clayton 2003, Pearson 1999, Zwolak and Foresman 2007, 2008). Deer mice (*Peromyscus maniculatus*) are known to be voracious seed predators, particularly in disturbed stands (Gashwiler 1967, Sullivan 1979, Sullivan and Sullivan 1982, 2004, Tallmon et al. 2001), yet their impact on natural forest regeneration remains largely unknown. Even heavy seed predation does not necessarily lead to a reduction in seedling abundance; for example when populations are limited by the number of available microsites (“establishment limitation”) rather than by the number of surviving seeds (Andersen 1989, Crawley 1992, Clark et al. 2007).

In this study, we experimentally examined the magnitude of seed predation by deer mice and its impact on conifer recruitment in wildfire-burned and unburned forest stands in western Montana. We focused on tree species dominant across many forests in western North America: ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*). In both burned and unburned forest, we (1) quantified deer

mouse abundance and seed removal, (2) determined whether removal rates were higher for larger ponderosa pine seeds than for smaller Douglas-fir seeds, and (3) investigated the effects of seed removal on seedling recruitment. Together, these analyses assess and compare the effects of fire vs. mice on the composition and rate of conifer recruitment.

## Materials and Methods

### Study site

We conducted this research within montane forest on the Lolo National Forest in west-central Montana, U.S.A., approximately 50 km west of Missoula. The dominant species was Douglas-fir, followed by ponderosa pine, lodgepole pine (*Pinus contorta*), and western larch (*Larix occidentalis*). In the summer of 2005, the I-90 wildfire burned 4550 ha of the forest. In the spring of 2006, we selected three pairs of study sites, each pair consisting of one stand that was burned with a stand-replacement fire (100% tree mortality and removal of litter layer) and one located in unburned forest of similar elevation (1600-1900 m) and aspect (south- or west-facing). Distances between the stands ranged from 0.85 to 5.5 km. Each stand was located at least 50 m from different habitat types.

### Deer mouse trapping

We conducted trapping in 2006 and 2007 from June to August in monthly sessions, each consisting of 4 consecutive nights of trapping (with minor adjustments of this schedule due to adverse weather). Each sampling grid consisted of 169 trapping stations, spaced 10 m apart and arranged in a 13 by 13 square (grid area = 1.44 ha). One folding Sherman<sup>TM</sup> live trap was placed at each trapping station, baited with rolled oats, and supplied with polypropylene batting. To target deer mice, which are nocturnal, we set traps in the evening (~6:00 pm) and closed them upon checking in the morning each day before 10:00 am. Captured rodents were identified to species, weighed, sexed, individually marked using ear tags, and released at the trap station.

### Seed removal experiments

In 2006 and 2007, we used seed removal experiments to estimate relative levels of seed predation. Experiments were conducted in September, after trapping to avoid confounding results with the presence of baited traps. In 2007, experiments at

the last pair of sites were delayed due to intense rainfall, and were eventually conducted under adverse weather conditions (very low temperature and overnight snowfall) and therefore were not included in the analysis below. Within each trapping grid, we put out 40 seed offerings, each consisting of a Petri dish (150x33 mm) filled with a mixture of 125 ml of sand and 20 seeds. Dishes were spaced at 20 m intervals at locations corresponding to locations of every second trap station. At each grid, half of the dishes contained ponderosa pine seeds, and half contained Douglas-fir seeds, all locally collected. Dishes were arranged in an alternating, checkerboard pattern by seed species. We presented seed offerings for two days and two nights and examined them shortly after sunrise (~0630 hrs) and before sunset (~1930 hrs) each day. This way, we could differentiate removal by nocturnal deer mice and diurnal granivores such as chipmunks (*Tamias* spp.) and red squirrels (*Tamiasciurus hudsonicus*). If a seed offering had signs of foraging (disturbed sand surface, broken seed shells, feces), we counted the remaining intact seeds and filled the dish with fresh sand and new seeds. When feces were found, we recorded their presence and identified them as “deer mouse” or “other” rodents. Captures of other similarly sized rodent were extremely rare in burned forest. In unburned forest, red-backed voles (*Myodes gapperi*) were relatively common, but due to the higher proportion of green plants in their diet, red-backed vole feces are very distinct. Feces of other granivores such as chipmunks or red squirrels are noticeably larger than those of deer mice.

#### Seedling recruitment trials

To address the effects of deer mouse seed predation versus fire on relative rates of seedling recruitment (gauged by seedling emergence and establishment) of ponderosa pine and Douglas-fir, we sowed seeds in 20 x 20 x 20 cm wire mesh cages. Half of the cages had 3 x 6 cm holes cut in each side to allow access of deer mouse-sized rodents, while the other half remained enclosed to prevent access. Cages were spaced 0.5 – 1.5 m apart in sets of two (one enclosed and one allowing access), and ten locally collected seeds were added to each cage, with seed species randomly assigned to each pair. Cages were buried 10 cm into the ground and topsoil was removed and replaced with mineral soil dug out from a depth of 0.25-0.5 m to minimize presence of an ambient seedbank. In the unburned forest, the soil was then covered with litter of the same thickness as that found adjacent to the cages. In the burned forest, there was no litter present.



Eight pairs of cages were set out at 40-m intervals along two transects parallel to and located ~10 m from the opposite edges of each trapping grid. In 2006, we added seeds to the surface during September when natural seed rain occurs. We quantified new seedlings the following June, when emergence was complete (no new seedlings were found subsequently). We defined establishment as the *proportion* of seedlings that survived until September. We then repeated the experiment for another year by pulling seedlings, replacing the soil, and adding new seeds.

### Statistical Analysis

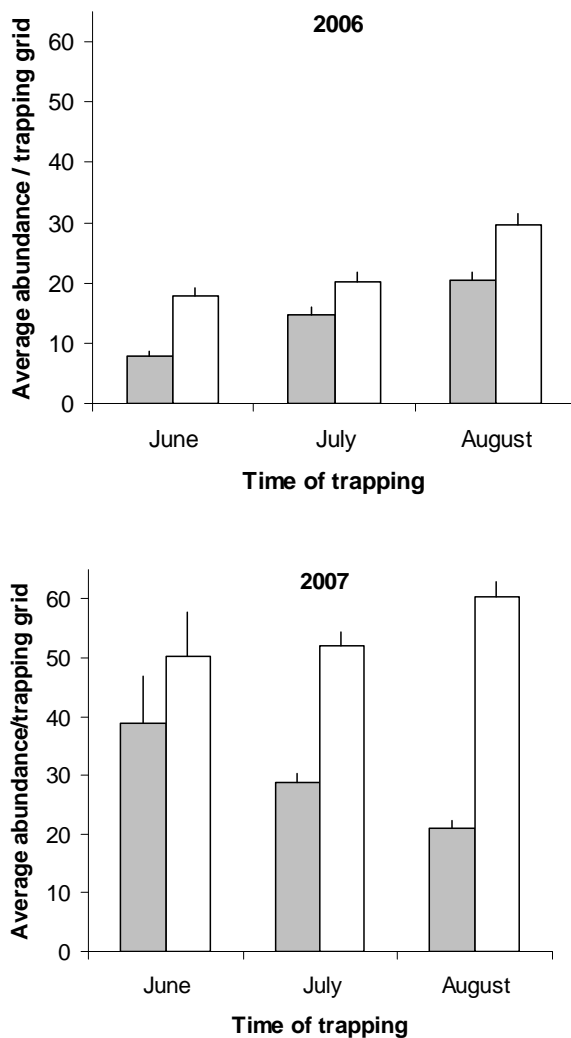
We estimated abundance of deer mice per site and month using program MARK (White and Burnham 1999). We used Huggins closed robust design (Huggins 1989, 1991) because of its good performance given sparse data (Conn et al. 2006). The most parsimonious models were determined with Akaike's information criterion corrected for small sample size ( $AIC_c$ ). Estimation of parameters followed Zwolak and Foresman (2008). The effective sampling area of trapping grids (estimated with mean maximum distance moved: White et al. 1982) did not differ between burned and unburned forest (Chapter 4). Abundance estimates were model-averaged according to Akaike weights ( $w_i$ , Burnham and Anderson 2002). To derive overall deer mouse abundance in burned and unburned forest for each month, we averaged estimates from respective trapping sites. For yearly estimates, we averaged abundance across months, with standard error reflecting sample variance derived using the Delta method (Seber 1982:138, Zwolak and Foresman 2008).

Seed removal and seedling recruitment were analyzed with logistic regression models (function "lmer") in R (R Development Core Team 2006). Fixed effects included fire (burned versus unburned), seed species, rodent access (i.e. open versus closed cages, seedling establishment models only), and day (i.e. first or second, seed removal models only). Random effects included study site and either cage (seedling establishment models) or trap station (seed removal trials). We analyzed daytime and nighttime seed removal separately. In each case, we began with a model containing all the above-mentioned variables and their interactions, and the structure of the final model was determined through stepwise regression with backward elimination of non-significant ( $P > 0.05$ ) variables.

## Results

### Deer mouse abundance

Estimated mean abundance of deer mice was 1.6 times higher in burned compared to unburned forest in 2006 ( $22.6 \pm \text{SE of } 0.9$  versus  $14.3 \pm 0.5$  mice/site), and 1.8 times higher in burned compared to unburned forest in 2007 ( $54.2 \pm 2.8$  versus  $29.5 \pm 2.7$  mice/site; Fig. 1). However, there was considerable variation in deer mouse abundance, particularly in unburned forest (Table 2 in Chapter 4).



**Fig. 1.**—Average abundance of deer mice in burned (open columns) and unburned (filled columns) sites in 2006 and 2007. Bars denote standard errors based on sample variance.

## Seed removal

Seed removal at night was higher in burned versus unburned forest, particularly in 2008 (fire and fire x year effects: Table 1a; Figure 2A). In addition, more ponderosa pine than Douglas-fir seeds were removed at night (species effect: Table 1a; Fig. 2A).

During the day, overall differences in removal between burned and unburned forest were not significant. However, in contrast to nighttime, daytime removal was less intense in burned versus unburned forest in 2007 (fire x year effect: Table 1b; Fig. 2B). As in nighttime trials, removal of ponderosa pine seeds was more severe than Douglas-fir seeds, though this was only significant in 2007 (species x year effect: Table 1b; Fig. 2B).

Deer mouse feces were found in 66% and 30% of trays with missing seeds in burned and unburned sites, respectively. Feces of other species (red squirrels, *Tamiasciurus hudsonicus*, and chipmunks, *Tamias* spp.) were found in only a few trays. Although not quantified, a substantial proportion of seed was eaten on the spot, as evidenced by broken seed shells left in the vicinity of seed trays (Plate 1).



**Plate. 1.**— Seed removal experiment: undisturbed (left) and disturbed (right) offering of Ponderosa pine (*Pinus ponderosa*) seeds. Arrow denotes broken seed shells. Photo credit R. Zwolak.

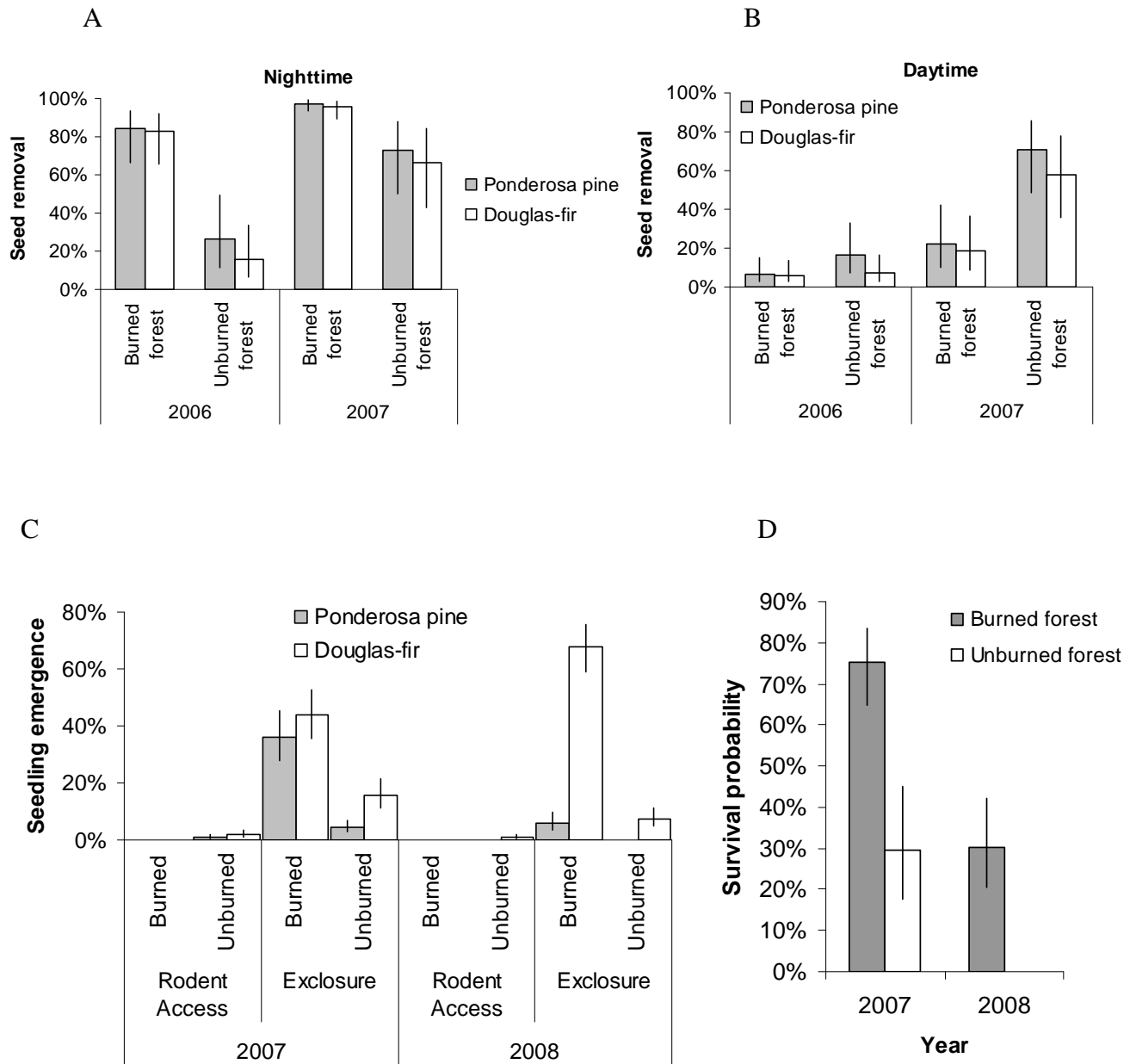
### Seedling recruitment

Seedling emergence in closed cages (Plate 2) was considerably higher in burned versus unburned stands (fire effect: Table 2), but this effect disappeared where rodents could access seeds (rodent access x fire effect: Table 2). In cages without rodent access, 39% of seedlings emerged in burned forest versus 7% in unburned forest, while in cages with access, 0% of seedlings emerged in burned forest versus 0.9% in unburned forest (Fig. 2C). Overall, fewer ponderosa pine seedlings than Douglas-fir emerged (species effect: Table 2).

Seedling survival also differed strongly between burned and unburned forest ( $z = 2.83$ ,  $P = 0.005$ ). In 2007, 75% (55 out of 73) of seedlings in burned forest survived until September, whereas survival in unburned forest was only 30% (8 out of 27 seedlings survived) In 2008, the overall pattern of higher survival in burned forest remained unchanged, but the establishment in both burned (30%: 23 out of 76 seedlings) and unburned (0 out of 10 seedlings) forest was lower than in 2007 ( $z = -5.27$ ,  $P < 0.0001$ ). Besides fire and year, no other factors were significant predictors of seedling survival.



**Plate 2.**—Douglas-fir (*Pseudotsuga menziesii*) seedlings in a closed cage in burned forest.



**Fig. 2.**—Deer mouse seed removal and its impact on the recruitment of ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) in burned and unburned forest. Bars denote standard errors. (A) Nighttime seed removal. (B) Daytime seed removal. (C) Seedling emergence. “Access” indicates emergence in germination cages with openings and “Exclosure” denotes emergence in closed germination cages. Seedlings were not found in “access” cages in burned forest. (D) Seedling survival. Survival did not differ between species, thus data on ponderosa pine and Douglas-fir were pooled.

**Table 1.**—Results of logistic regression for nighttime (a) and daytime (b) seed predation trials.

a. Overnight seed predation

Variable <sup>1</sup>	Regression coefficient ( $\pm$ SE)	<i>z</i> -value ( <i>P</i> )
Intercept	-4.44 $\pm$ 0.92	-4.80 (<0.0001)
<i>Fire</i>	5.59 $\pm$ 1.28	4.38 (<0.0001)
<i>Day</i>	0.73 $\pm$ 0.05	13.45 (<0.0001)
<i>Species</i>	1.16 $\pm$ 0.32	3.70 (0.0002)
<i>Year2007</i>	2.60 $\pm$ 0.08	34.92 (<0.0001)
<i>Fire*Year2007</i>	-0.82 $\pm$ 0.15	5.56 (<0.0001)

b. Seed predation during daytime

Variable	Regression coefficient ( $\pm$ SE)	<i>z</i> -value ( <i>P</i> )
Intercept	-6.85 $\pm$ 1.50	-4.55 (<0.0001)
<i>Fire</i>	-2.92 $\pm$ 2.11	-1.38 (0.167)
<i>Day</i>	0.87 $\pm$ 0.06	14.01 (<0.0001)
<i>Species</i>	0.91 $\pm$ 0.54	1.70 (0.090)
<i>Year2007</i>	4.02 $\pm$ 0.13	30.23 (<0.0001)
<i>Fire*Year2007</i>	-2.84 $\pm$ 0.15	-18.70 (<0.0001)
<i>species*Year2007</i>	0.62 $\pm$ 0.15	4.17 (<0.0001)

<sup>1</sup> *Fire* indicates burned versus unburned forest, *Day* denotes the change in seed removal rates during the second day of the trials, *Species* is the removal of ponderosa pine, *Pinus ponderosa*, relatively to Douglas-fir, *Pseudotsuga menziesii*, and *Year2007* is the seed removal during the in 2007 relatively to that in 2006. See the text for further explanation.

**Table 2.**—Results of logistic regression for seedling emergence trials.

Variable <sup>1</sup>	Regression coefficient ( $\pm$ SE)	z-value ( <i>P</i> )
Intercept	-2.28 $\pm$ 0.37	-6.08 (<0.0001)
<i>Fire</i>	2.01 $\pm$ 0.45	4.47 (<0.0001)
<i>Rodent access</i>	-2.23 $\pm$ 0.74	-3.01 (0.0026)
<i>Species</i>	-0.87 $\pm$ 0.44	-2.00 (0.046)
<i>Year2007</i>	-0.82 $\pm$ 0.42	-1.94 (0.053)
<i>Fire*Year2007</i>	2.27 $\pm$ 0.53	4.28 (<0.0001)
<i>Fire*Rodent access</i>	-3.82 $\pm$ 1.22	-3.12 (0.0018)
<i>spPP*Year2007</i>	-3.59 $\pm$ 0.61	-5.87 (<0.0001)

<sup>1</sup> *Fire* indicates burned vs. unburned forest, *Rodent access* denotes emergence in open cages, *Species* is the emergence of ponderosa pine (*Pinus ponderosa*) seedlings relatively to that of Douglas-fir (*Pseudotsuga menziensis*), and *Year2007* is the emergence during the second year of the cage germination trials. See the text for further explanation.

### Discussion

Our results demonstrate that wildfire creates highly favorable conditions for seedling recruitment, but that intense seed predation by elevated deer mouse populations reduces this effect. Deer mice were probably responsible for the seed loss in burned forest because (1) deer mice accounted for 86% of individuals captured in the burned forest (Chapter 4), and (2) seed removal in burned forest was intense only at night, when chipmunks, the only other rodents that were regularly captured in burned forest, do not forage. In addition, signs of foraging and feces left on most depredated seed trays indicated seed removal by mice. Since the striking difference between seedling emergence in open and closed cages suggest strong seed limitation in burned forest, seed predation by deer mice might affect the process of postfire forest succession.

Mice are known to increase in abundance after forest disturbances, including wildfire (Pearson 1999, Fisher and Wilkinson 2005, Chapter 2 of this dissertation) and for their ability to control plant populations through intense seed consumption (Kauffman and Maron 2006, Pearson and Callaway 2008). However, our study is the first to demonstrate that mice reduce seedling recruitment in burned forest. This ecological effect may be unique to the postfire succession in western North America. For example, in *Pinus coulteri* woodlands in coastal California, where the small-mammal community is dominated by kangaroo rats (*Dipodomys agilis*), rodents substantially contributed to postfire seed dispersal and seedling establishment (Borchert et al. 2003). In *Pinus halepensis* forests in Spain, seed predation in burned areas was lower than in unburned areas and exclusion of rodents (probably *Apodemus* spp.) resulted in only moderate increase in seedling density (Broncano et al. 2008).

It is possible that some of the seeds removed from the seed trays and germination cages were cached rather than eaten (Vander Wall et al. 2005, Moore and Swihart 2008). Even though deer mice are thought to act as seed predators rather than seed dispersers (Sullivan 1978), some individuals do cache seeds (Vander Wall 1992, Vander Wall et al. 2001). Therefore, our estimates of seed removal may be considered the upper boundary of seed mortality caused by deer mice. In undisturbed habitats, germination from uneaten seeds that were scatter hoarded is usually higher than germination from the litter surface (Vander Wall 1992), probably because litter acts as a mechanical barrier preventing seed-soil contact (Castro et al. 2002). Taking into account the possibility of germination from caches, the effect of mice on tree recruitment in unburned forest could actually be positive. This would require that the unmeasured fraction of removed seeds that remains uneaten, germinates, and establishes, is higher than the fraction of seeds that emerged and established in closed cages in unburned forest (germination x establishment = 0-5%; see Figure 3). In burned forest, a high fraction of seeds sowed on the ground surface in closed cages emerged and survived. It is unlikely that caching by mice could further improve germination and survival. Naturally occurring seedlings in burned forest were rare and seedling clumps, a tell-tale sign of germination from rodent caches (Vander Wall 1992, Borchert et al. 2003), were never found. Overall, it appears that there is little benefit from deer mouse-mediated seed dispersal in burned forest, and the costs of seed removal are high. Thus, deer mice serve mostly as seed predators in burned forest, although it is possible that they function as seed dispersers in unburned forest.



If this is the case, the role of deer mice in tree recruitment would be context-dependent.

Deer mice demonstrated slight but significant preference for larger ponderosa pine over smaller Douglas-fir seeds. However, seed removal in burned forest was so intense that no seedlings were found in open germination cages, regardless of sowed species. Therefore, other than slowing down the rate of reestablishment, the impacts of mice in burned forest are difficult to predict.

Our results serve as a prominent example of how vertebrates mediate the effects of the physical environment on plant communities. Deer mice alter seedling establishment and may act as drivers of postfire succession of western forests. This situation represents an unforeseen, indirect effect of forest fires, and a disturbance-mediated “top-down” effect of rodents on plant communities.

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## ADDENDUM

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**Ogniu, kroc za mną:**

**Ekologia i polityka**

**pożarów lasów Ameryki Północnej**

Fire, walk with me:

Ecology and politics

of forest fires in North America

### 1. Wstęp

Zaburzenia ekologiczne to nieodłączna część ekologicznych procesów. Wiatrołomy, inwazje owadów („szkodników”), powodzie, pożary, ekstremalne susze charakteryzują i kształtują ekosystemy w takim samym, a często nawet większym stopniu, niż przeciętna temperatura, czy średnie opady (White i Pickett 1985). W dodatku zaburzenia, o ile nie są zbyt częste i silne, mogą zwiększać różnorodność biologiczną. Przy ich braku, ekosystemy zdominowane są przez organizmy przystosowane do nasilonej konkurencji międzygatunkowej. Przy częstych, silnych zaburzeniach, prym wiodą gatunki odporne na stres i zdolne do szybkiej kolonizacji siedlisk. Natomiast pośrednia częstotliwość i siła zaburzeń sprzyja współistnieniu obu strategii życiowych (Connell 1978). Niektórzy ekolodzy kwestionują uniwersalność tego scenariusza (np. Mackey i Currie 2001), lecz znakomita większość zgadza się, że zaburzenia są jednym z najważniejszych czynników kształtujących różnorodność biologiczną.

Choć ludzie czasem powodują nasilenie naturalnych zaburzeń i sami bywają ich czynnikiem, to zwykle starają się je kontrolować, powstrzymywać i tłumić. Czasami w najlepszej wierze głęboko zmieniamy przy tym funkcjonowanie ekosystemów i nierzadko sprowadzamy na siebie mnóstwo nieprzewidzianych kłopotów. W artykule tym opisuję właśnie takie problemy i sposoby radzenia sobie z nimi na przykładzie pożarów lasów iglastych Ameryki Północnej.

## 2. Rola pożarów w ekologii lasów iglastych

### Ameryki Północnej

Ogień to najważniejsze naturalne zaburzenie w lasach Północy, kształtujące je od tysięcy (Hansson 1992), a nawet milionów lat (Weber i Taylor 1992). Pożary odpowiadają za naturalną strukturę tych lasów, które tworzą unikalną mozaikę różnych stopni sukcesji, niezwykle *patchwork*, w którym wiele gatunków roślin i zwierząt występuje tylko w specyficznych siedliskach powstających po upływie określonego czasu od zaburzenia. Stożące pnie spalonych drzew, powalone kłody, nory powstałe w miejscu wypalonych korzeni i pokryta sadzą gleba oferują unikalne siedliska wysoce wyspecjalizowanym, „pożarolubnym” gatunkom roślin i zwierząt. Las po intensywnym pożarze wygląda jak cmentarzysko, ale dla wielu organizmów jest doskonałym, a czasem nawet jedynym siedliskiem. Ciemniki, chrząszcze z rodzaju *Melanophila* (bogatkowate, Buprestidae), wykrywają pożary z odległości nawet 50 kilometrów (mechanizm opisują Schütz i in. 1999), kierują się w ich stronę i składają jaja w świeżo spalonym drewnie – jedynym środowisku, gdzie mogą rozwijać się ich larwy. Dzieńcioły północne (*Picoides arcticus*) żywią się owadami zjadającymi drewno spalonych drzew i rzadko spotykane są w siedlisku innym, niż niedawno zniszczony przez pożar las (Hutto 1995). Także dla wielu gatunków eurytopowych pożary wcale nie są katastrofą: np. wszędobyłski myszak amerykański *Peromyscus maniculatus* gwałtownie zwiększa liczebność populacji po pożarach lasu (Zwolak i Foresman 2007). Również drzewa zaadaptowały się do powtarzających się pożarów. Niektóre, wyposażone w niezwykle grubą korę, bez szwanku wytrzymują umiarkowane pożary (np. sosna żółta *Pinus ponderosa* lub sekwoja wiecznie zielona *Sequoia sempervirens*). Inne potrzebują ognia, aby się rozmnożyć: np. szyszki sosny wydmowej *Pinus contorta* otwierają się dopiero pod wpływem wysokiej temperatury (Miller 2000). W nieobecności pożarów gatunki te zwykle przegrywają w konkurencji z mniej odpornymi, ale szybko rosnącymi drzewami. Krótko mówiąc, większość lasów Ameryki Północnej zostało ukształtowanych przez powtarzające się pożary. Nam, mieszkańcom strefy umiarkowanej Europy, gdzie pożary lasów są rzadkością, trudno sobie to nawet wyobrazić.

### 3. Iskrzenie na styku polityki i ekologii

#### 3.1. Czy uda się „wyleczyć” lasy Stanów Zjednoczonych Ameryki Północnej?

Pożary to naturalne zjawisko w lasach Ameryki Północnej. Od tysięcy lat wywołują je uderzenia piorunów podczas tzw. „suchych burz”, częstych np. za zachodzie Stanów Zjednoczonych. Również wiele indiańskich plemion celowo wznicało pożary lasu, wzmagając ich częstotliwość na niektórych obszarach dzisiejszych USA i Kanady (Swetnam i Baisan 1996). Wraz z zasiedleniem Ameryki przez białego człowieka, postrzegającego pożary lasu jako nieprzewidywalne, groźne i jednoznacznie negatywne zjawisko, rozpoczęła się era intensywnego ich zwalczania. Bezpośrednim impulsem do nasilonej walki z pożarami były *The Great Fires*, pożary które spustoszyły Góry Skaliste w 1910 r., niszcząc liczne domy i zabijając wielu ludzi. W efekcie, główną misją formującej się dopiero amerykańskiej służby leśnej (*USDA Forest Service*) stało się od tej pory powstrzymywanie i gaszenie pożarów lasu (Paine 2001). *The Great Fires* wywołały zażartą debatę pomiędzy zwolennikami bezwzględnego zwalczania ognia oraz zwolennikami stosowania kontrolowanych pożarów do utrzymywania lasów o pożądanym składzie gatunkowym. Koncepcja używania ognia jako metody gospodarowania była wzorowana na działaniach Indian, stąd nazwana została pogardliwie „indiańskim leśnictwem” (Paine 2001). W następstwie *The Great Fires*, opcja ta z kretesem przegrała.

Przez lata wydawało się, że polityka gaszenia wszystkich pożarów w zarodku odnosi spektakularny sukces. Jednak już w latach 60. naukowcy i leśnicy dostrzegli, że sukces ten opłacono wieloma niekorzystnymi zmianami ekologicznymi: inwazjami egzotycznych gatunków roślin, zanikiem wielu rodzimych i głębokimi zmianami w strukturze lasów (Convington 2000, Stephens i Ruth 2005). W dodatku, pomimo wciąż wzrastających sił i środków przeznaczanych na walkę z pożarami lasu, ich liczba i obszar drastycznie wzrosły w ostatnich latach (rys. 1). Według niektórych ekspertów (zobacz np. Convington 2000), paradoks ten jest wywołany nagromadzeniem martwego drewna oraz zmianami gatunkowymi i wzrostem gęstości drzewostanów, które nastąpiły po wyeliminowaniu pożarów. Pożary w tak zmienionych lasach są niezwykle intensywne. Swetnam i Baisan (1996) mówią o paradoksie walki z tym żywiołem: „jeżeli na krótką

metę odnosimy sukces w redukowaniu liczby pożarów poniżej pewnego poziomu, wtedy wcześniej lub później następują katastrofalne, niszczące pożary”.

Rozwiązaniem tego problemu ma być *Healthy Forest Restoration Act*, podpisany przez prezydenta George’a W. Busha w 2003 r. Ustawa ta zakłada zmniejszenie gęstości drzewostanów poprzez selektywną wycinkę drzew oraz redukcję nagromadzonych paliw (tzn. martwego drewna) poprzez zastosowanie kontrolowanych pożarów (USDA Forest Service 2003). Mimo że koncepcja ta spotkała się z krytyką naukowców, organizacji ekologicznych i wielu leśników, jest obecnie wcielana w życie na rozległych obszarach wielu zachodnich stanów. Organizacje ekologiczne zarzucają, że *Healthy Forest Restoration Act* jest wygodną furtką pozwalającą wpływowym kompaniom przemysłu drzewnego na wycinkę nawet najstarszych drzewostanów. Naukowcy z kolei wskazują, że ustawa ta stosuje jeden sposób postępowania, oparty wyłącznie na badaniach lasów zdominowanych przez sosnę żółtą, do każdego typu lasu, niezależnie od jego składu gatunkowego. Tymczasem lasy Ameryki Północnej cechuje ogromne zróżnicowanie typów, intensywności i częstotliwości naturalnych pożarów. W uproszczeniu, lasy sosny żółtej, położone na niższych wysokościach i na niższych szerokościach geograficznych, odznaczają się częstymi pożarami poszycia, natomiast dla lasów wysokogórskich i borealnych charakterystyczne są rzadsze pożary koron, które powodują wysoką (często 100%) śmiertelność drzew. Badania wskazują, że polityka powstrzymywania pożarów, w połączeniu z intensywnym pozyskiwaniem drewna, rzeczywiście wywołała szereg niekorzystnych zmian w lasach historycznie zdominowanych przez sosnę żółtą (Schoennagel i in. 2004). W ekosystemach tych zwiększył się udział drzew cieniulubnych, które rosną w dużym zagęszczeniu (np. jedlica zielona *Pseudotsuga menziesii*) i w efekcie znacznie zwiększają częstotliwość intensywnych pożarów koron. Z drugiej strony, polityka powstrzymywania pożarów nie miała wpływu na funkcjonowanie lasów wysokogórskich. Tam pożary również są naturalnym, bardzo ważnym zjawiskiem, lecz występują z mniejszą częstotliwością (co 100–200 lat: Arno 2000) i ludzkie działania trwały zbyt krótko, by znacząco te ekosystemy zmienić. W tej sytuacji selektywna wycinka proponowana w *Healthy Forest Restoration Act* jest zbędna, ponieważ nie zredukuje prawdopodobieństwa pożarów, a jedynie zakłóci naturalne funkcjonowanie lasu (Schoennagel i in. 2004). Wreszcie Stephens i Ruth (2005)

wykazali, że cele *Healthy Forest Restoration Act* są nierealistyczne, ponieważ zabraknie środków i czasu, aby przeprowadzić selektywną wycinkę i kontrolowane pożary na olbrzymich obszarach (25 milionów ha), które tych działań rzeczywiście potrzebują.

### **3.2 Czy warto wycinać spalony las?**

Konsekwencją postrzegania pożarów jako ekologicznej i ekonomicznej katastrofy, a spalonych drzew jako marnującego się drewna, jest praktyka *salvage logging*, czyli w wolnym tłumaczeniu „zrębu ratunkowego”: usuwania po pożarze stojących, martwych drzew. Zrąb taki ma na celu (1) „uratowanie” części straconego w pożarze drewna, (2) przyspieszenie regeneracji lasu oraz (3) zredukowanie ryzyka przyszłych pożarów poprzez zmniejszenie ilości martwego drewna. Praktyka ta jest kontrowersyjna, ponieważ pnie spalonych drzew są ważnym siedliskiem dla wielu gatunków zwierząt i roślin (Lindenmayer i in. 2004, Nappi i in. 2004). Co więcej, zrąb popożarowy poważnie zaburza stosunki wodne oraz przyczynia się do gwałtownej erozji gleby (Karr i in. 2004). Wreszcie drogi budowane, by umożliwić wyrąb i wywóz spalonych drzew powodują długotrwałe zmiany w strukturze roślinności i przyczyniają się do rozprzestrzeniania gatunków inwazyjnych (Beschta i in. 2004). Najgłośniejszym echem odbiły się wyniki badań Donato i in. (2006) z wydziału leśnictwa *Oregon State University*, opublikowane w prestiżowym magazynie *Science*. Wykazały one, że dwa z trzech wyżej wymienionych argumentów za przeprowadzaniem zrębu popożarowego nie znajdują odzwierciedlenia w faktach. Użycie ciężkiego sprzętu do wycinki poważnie uszkadza glebę, niszczy siewki drzew i zamiast przyspieszać, znacząco spowalnia regenerację lasu. W dodatku, zrąb zwiększa zamiast zmniejszać ryzyko przyszłych pożarów, ponieważ jego uboczny produkt to duża ilość martwego drewna na powierzchni gleby.

Publikacja ta wywołała ogromne kontrowersje, ponieważ ukazała się w momencie, gdy do amerykańskiego Kongresu trafiły dwie ustawy ułatwiające kompaniom drzewnym zrąb popożarowy na terenie lasów państwowych. Jednak prawdziwy skandal nastąpił, gdy wyszło na jaw, że władze wydziału leśnictwa *Oregon State University* usiłowały wpłynąć na redaktorów *Science*, by zatrzymać publikację swoich podwładnych. Pikanterii dodaje fakt, że 12% budżetu wydziału pochodzi z dotacji od przemysłu drzewnego (Stokstad 2006). Do dyskusji włączył się także kongresman Brian N. Baird, z wykształcenia... psycholog, który – również na łamach *Science* – skrytykował metody

zastosowane w badaniach Donato (Baird 2006). Wreszcie Donato i pozostali autorzy badań poproszeni zostali o zrelacjonowanie swoich wyników przed komisją senacką, stawiając czoła wielu dociekliwym, czy wręcz napastliwym pytaniom (Stokstad 2006). Tymczasem rezultaty badań Donato i in. (2006) trudno uznać za zaskakujące. Już wcześniejsze badania wskazywały na szkodliwe efekty zrębu popożarowego (przegląd w Karr i in. 2004 oraz w Nappi i in. 2004). Wyniki te ukazały się jednak w bardziej wyspecjalizowanych i mniej prestiżowych czasopismach.

Całkowite zaprzestanie zrębu popożarowego jest niezbyt prawdopodobne ze względów ekonomicznych. Jego negatywne skutki mogą (i powinny) być jednak zminimalizowane. Naukowcy postulują szereg rozwiązań, wliczając w to pozostawianie niektórych spalonych drzew (zwłaszcza tych największych), wzmożenie wysiłków mających na celu chronienie gleby podczas operacji wycinania i wywozu drzew, unikanie tworzenia nowych dróg, ograniczanie sztucznego zalesiania spalonych obszarów, czy wreszcie krytyczny postulat monitorowania wyników gospodarki popożarowej (Hutto 1995, Beschta i in. 2004, Karr i in. 2004). W cennych ekologicznie rejonach „zręb ratunkowy” w ogóle nie powinien być przeprowadzany (Karr i in. 2004).

### **3.3. Czy zręb zupełny może zastąpić naturalne zaburzenia w lasach Kanady?**

W Kanadzie polityka gaszenia naturalnych pożarów połączona z intensywną gospodarką leśną sprawiły, że zręb zupełny zastąpił pożary jako dominujące zaburzenie lasów borealnych. W tym samym czasie nastąpiła ważna zmiana w postrzeganiu lasu przez społeczeństwo Kanady: puszcze borealne nie są już traktowane wyłącznie jako miejsce produkcji drewna, ale jako skomplikowane, dynamiczne ekosystemy, które są siedliskiem dla wielu organizmów (wliczając w to zwierzynę łowną), służą jako miejsce wypoczynku i dostarczają niełatwych do przeliczenia na pieniądze wrażeń estetycznych (Mitchell i Beese 2002). W efekcie większość społeczeństwa nie akceptuje już wielkoobszarowych zrębów zupełnych (Pâquet i Bélanger 1997), choć to właśnie ta metoda pozyskiwania drewna jest najbardziej ekonomiczna i z tego powodu najczęściej stosowana (Keenan i Kimmins 1993). Czy jednak niechęć ta jest uzasadniona? W końcu wycinka to również zaburzenie, tak jak ogień, do którego lasy borealne są od tysięcy lat zaadaptowane. Idąc tym tropem, niektórzy naukowcy twierdzą, że jeśli uda się

zmodyfikować metody pozyskiwania drewna tak, żeby jego skutki ekologiczne przypominały efekty pożarów, funkcjonowanie, struktura i różnorodność biologiczna eksploatowanego lasu pozostanie nienaruszona (np. Ehnes i Keenan 2002). Teza ta leży u podstawy nowego paradygmatu w leśnictwie Kanady, tzw. *emulation forestry*, czyli gospodarki leśnej symulującej skutki naturalnych zaburzeń. Zrąb powinien więc zachodzić z częstotliwością podobną do częstotliwości pożarów, na obszarach zbliżonych do obszarów pożarów, i z intensywnością (mierzoną wpływem na organizmy żywe) przybliżoną do tej, która charakteryzuje pożary (szczegółowe zalecenia znaleźć można np. w Ehnes i Keenan 2002). Koncepcja ta zdobyła w Kanadzie dużą popularność, także dlatego, że stanowi usprawiedliwienie dla wyrębu olbrzymich połąci lasu (McRae i in. 2001). Areał naturalnych pożarów lasu ma charakterystyczny rozkład, z wieloma małymi i nielicznymi o bardzo dużej powierzchni lasów (Stocks i Simard 1993). I to właśnie ta cecha jest najchętniej naśladowana w raczkującej *emulation forestry*. W tej sytuacji trudno przypuszczać, żeby ta nowa praktyka była receptą na utrzymanie wysokiej różnorodności biologicznej w eksploatowanych lasach. Jednak nawet dużo bardziej wyrafinowane wersje *emulation forestry* ignorują szereg zasadniczych różnic pomiędzy skutkami pożarów i zrębu (za McRae i in. 2001):

1. Zrąb to zaburzenie mechaniczne, natomiast pożar to gwałtowna reakcja chemiczna.
2. Pożary zwiększają ilość martwego drewna, pełniącego ważne role ekologiczne (patrz wyżej), podczas gdy skutkiem (i celem) zrębu jest wywóz drewna z lasu.
3. Pożary użyźniają glebę; zrąb zwykle powoduje jej degenerację.
4. Pozyskiwanie drewna przyczynia się do rozwoju sieci dróg w lesie, co pociąga za sobą jego fragmentację, nasilone użytkowanie przez ludzi, inwazje egzotycznych gatunków roślin oraz erozję gleby.
5. Sukcesja po pożarze i po zrębie przebiega zupełnie innymi drogami: ta druga prowadzi często do długotrwałej dominacji gatunków liściastych.

Podsumowując, o ile możliwe jest zmodyfikowanie metod pozyskiwania drewna tak, by jego skutki przypominały efekty naturalnych pożarów, zaburzenia te nigdy nie będą równoznaczne. A skutki obecnej gospodarki leśnej są od skutków pożarów diametralnie



różne. Tym niemniej, *emulation forestry* uznać można za pozytywną tendencję w gospodarce leśnej, gdzie coraz większy nacisk kładzie się na utrzymanie różnorodności biologicznej i zachowanie integralności procesów ekologicznych. W końcu rezygnacja z pozyskiwania drewna jest niemożliwa. Nawet redukcja jego zużycia, choć ze wszech miar pożądana, pozostaje mrzonką (Dekker-Robertson i Libby 1998). W tej sytuacji, zmniejszenie rodzimej produkcji oznaczałoby konieczność wzmożonego importu drewna z zagranicy. Rozwiązanie to jest nieetyczne, bo oznacza przerzucenie związanych z tym problemów ekologicznych na inne kraje, najczęściej rozwijające się, gdzie pozyskiwanie drewna ma nierzadko charakter rabunkowy (Dekker-Robertson i Libby 1998). Dlatego ważne jest ciągle poszukiwanie nowych rozwiązań w kierunku samowystarczalnej gospodarki leśnej przy minimalnych kosztach dla środowiska. *Emulation forestry* jest jedną z takich prób.

#### **4. Zakończenie**

W ostatnich latach nastąpiła znacząca zmiana w nastawieniu wobec naturalnych pożarów lasu. Najpierw ekolodzy, potem leśnicy i wreszcie ogół społeczeństwa zaczął dostrzegać ogromne znaczenie zaburzeń ekologicznych w prawidłowym funkcjonowaniu wielu lasów Ameryki Północnej. Jednak stare problemy wciąż pozostają nierozwiązane, a do tego pojawiają się nowe. Polityka gaszenia wszystkich pożarów jest zbyt kosztowna i na dłuższą metę szkodliwa, ale nie można też ich totalnie akceptować, ponieważ w Stanach Zjednoczonych wciąż ogromnie popularne jest budowanie domów na samej granicy lasów. Ogień powoduje więc często ofiary śmiertelne i straty materialne. W dodatku polityka powstrzymywania pożarów okazała się drogą, z której nie ma powrotu: w niektórych ekosystemach nagromadziło się tyle paliw, że obecne pożary są niespotykane niszczące i wymagają zdecydowanych interwencji (Convington 2000). Wreszcie liczba pożarów w Ameryce Północnej wzrasta wraz z postępującym ocieplaniem klimatu i przewiduje się, że tendencja ta będzie się dalej nasilać (Westerling i in. 2006). Podsumowując, dynamika ekosystemów leśnych jest nieodwracalnie zmieniona, powrót do „naturalnych” warunków jest niemożliwy i większość obszarów leśnych wymaga lub będzie wymagać aktywnego gospodarowania. Problemem jest tylko ustalenie, jaki rodzaj działań będzie najskuteczniejszy.

**Podziękowania:** Stanisław i Julia Pagacz przeczytali pierwszą wersję artykułu, udzielając wielu cennych uwag.

### **Piśmiennictwo**

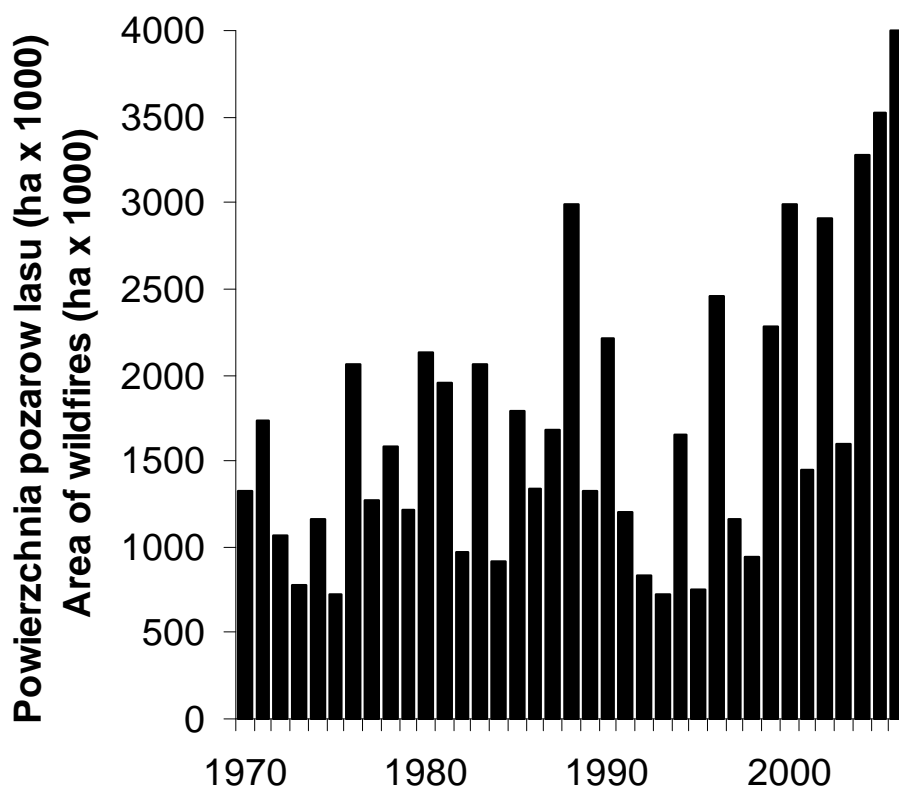
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## Summary

I reviewed the ecological and socio-political controversies associated with wildfires and forest management in North America. I focused on three management practices: (1) restoration of “healthy” forests in western US, (2) postfire (salvage) logging, and (3) the use of clearcutting to imitate natural disturbances (so called “emulation silviculture”). It has been argued that fire suppression in forests historically dominated by ponderosa pine (*Pinus ponderosa*) has resulted in changes in their structure and species composition, accumulation of fuels, and increased frequency and area of severe fires (Fig. 1). These problems are being addressed by thinning and prescribed burning, but implementing these actions in mid- and high-elevation forests is contentious because these forests have not been impacted by fire suppression. Salvage logging is intended to recoup economic losses, enhance regeneration and reduce fire risk. However, recent research indicates that postfire logging achieves only the first goal, while hindering regeneration and increasing woody fuel loads. Finally, forest harvest is unlikely to substitute wildfires because of differences in size distribution, frequency, and ecological consequences of the anthropogenic and natural disturbances. While the important ecological role of forest fires is being increasingly recognized, the management of fire-maintained forests is still facing unresolved problems. Moreover, the ongoing climate warming will make it even more challenging.



**Rys. 1.** Obszar pożarów lasu na terenie USA w latach 1970–2006 (na podstawie danych *National Interagency Fire Center*)  
 Area burned by wildfires in the United States between the years 1970–2006 (according to the National Interagency Fire Center)

**Appendix A.**—Studies used in “A meta-analysis of the effects of wildfire, clearcutting, and partial harvest on the abundance of North American small mammals”

<i>Reference</i>	<i>Study location</i>	<i>Forest type</i>	<i>Use in meta-analysis</i>
1. Buckner and Shure, 1985	North Carolina	Deciduous	Clearcutting: <i>P. maniculatus</i>
2. Campbell and Clark, 1980	Wyoming	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i>
3. Clayton, 2003	Utah	Coniferous	Clearcutting: <i>S. cinereus</i>
4. Clough, 1987	Maine	Coniferous, mixed	Wildfire, clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i> Clearcutting+burning: <i>M. gapperi</i>
5. Cockle and Richardson, 2003	British Columbia	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i>
6. Crête et al., 1995	Quebec	Coniferous	Wildfire: <i>M. gapperi</i> , <i>P. maniculatus</i>
7. Elliot and Root, 2006	Missouri	Deciduous	Clearcutting, partial harvest: <i>B. brevicauda</i> , <i>M. pennsylvanicus</i>
8. Ford and Rodrigue, 2001	West Virginia	Deciduous	Partial harvest: <i>S. cinereus</i> , <i>B. brevicauda</i> , Clearcutting (10-20 y.a.): <i>B. brevicauda</i>
9. Fuller et al., 2004	Maine	Mixed	Partial harvest: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>B. brevicauda</i> Clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>P.</i>

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			<i>maniculatus</i>
10. Gashwiler, 1970	Oregon	Coniferous	Clearcutting+burning: <i>M. gapperi</i> , <i>P. maniculatus</i>
11. Gitzen et al., 2007	Oregon	Coniferous	Partial harvest: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>P. maniculatus</i>
12. Gomez and Anthony, 1998	Oregon	Coniferous	Clearcutting: <i>P. maniculatus</i> , <i>M. longicaudus</i>
13. Gunther et al., 1983	Washington	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i>
14. Halvorson, 1982	Montana	Coniferous	Clearcutting+burning: <i>M. gapperi</i> , <i>P. maniculatus</i>
15. Healy and Brooks, 1988	West Virginia	Deciduous	Clearcutting: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>N. insignis</i> Clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>N. insignis</i>
16. Hooven, 1972	Oregon	Coniferous	Clearcutting, clearcutting+burning: <i>P. maniculatus</i>
17. Kirkland, 1974	West Virginia	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
18. Kirkland, 1977	West Virginia	Coniferous, deciduous	Clearcutting, clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>N. insignis</i> , <i>P. maniculatus</i> , <i>S. cinereus</i> Clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>N. insignis</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
19. Kirkland, 1978	Pennsylvania	Deciduous	Clearcutting: <i>M. gapperi</i>
20. Klenner and Sullivan, 2003	British Columbia	Coniferous	Clearcutting, partial harvest: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>T. amoenus</i>

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21. Krefting and Ahlgren, 1974	Minnesota	Mixed	Wildfire: <i>M. gapperi</i> , <i>P. maniculatus</i>
22. Kyle and Block, 2000	Arizona	Coniferous	Wildfire: <i>P. maniculatus</i>
23. Lovejoy, 1975	New England	Deciduous	Clearcutting: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>N. insignis</i> , <i>P. maniculatus</i> , Clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>N. insignis</i> ,
24. Martell, 1983	Ontario	Mixed	Partial harvest: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>N. insignis</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
25. Martell and Radvanyi, 1977	Ontario	Coniferous	Clearcutting: <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> ,
26. MacCracken, 2005	Washington	Coniferous	Partial harvest: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>P. maniculatus</i>
27. Medin, 1986	Idaho	Coniferous	Partial harvest: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>T. amoenus</i>
28. Medin, 1989	Idaho	Coniferous	Partial harvest: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>T. amoenus</i>
29. Mitchell et al., 1997	Virginia	Deciduous	Clearcutting: <i>B. brevicauda</i> , <i>P. maniculatus</i> , <i>S. cinereus</i> ,
30. Monthey and Soutiere, 1985	Maine	Coniferous	Clearcutting, partial harvest: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>N. insignis</i> , <i>P. maniculatus</i> Clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>N. insignis</i> , <i>P. maniculatus</i>
31. Pearce and Venier, 2005	Ontario	Coniferous, mixed	Clearcutting, clearcutting (10-20 y.a.): <i>B. brevicauda</i> , <i>M.</i>

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			<i>gapperi</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>N. insignis</i> , <i>S. cinereus</i>
32. Potvin et al., 1999	Quebec	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
33. Probst and Rakstad, 1987	Minnesota	Deciduous	Clearcutting: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
34. Ramirez and Hornocker, 1981	Montana	Coniferous	Clearcutting, clearcutting (10-20 y.a.), partial harvest: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
35. Ritchie et al., 1987	British Columbia	Coniferous	Clearcutting: <i>P. maniculatus</i>
36. Roppe and Hein, 1978	Colorado	Coniferous	Wildfire: <i>M. gapperi</i> , <i>P. maniculatus</i>
37. Simon et al., 1998	Labrador	Coniferous	Wildfire: <i>M. gapperi</i>
38. St-Laurent et al., 2008	Quebec	Coniferous	Clearcutting: <i>M. gapperi</i>
39. Steventon et al., 1998	British Columbia	Coniferous	Clearcutting, partial harvest: <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i>
40. Stout et al., 1971	Idaho	Coniferous	Wildfire: <i>P. maniculatus</i>
41. Sullivan, 1979a	British Columbia	Coniferous	Clearcutting+burning: <i>P. maniculatus</i>
42. Sullivan, 1979b	British Columbia	Coniferous	Clearcutting: <i>P. maniculatus</i>
43. Sullivan and Sullivan, 2001	British Columbia	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>S. cinereus</i> , <i>T. amoenus</i>

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44. Sullivan et al., 1999	British Columbia	Coniferous	Clearcutting+burning: <i>M. gapperi</i> , <i>P. maniculatus</i> Clearcutting: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>T. amoenus</i>
45. Sullivan et al., 2000	British Columbia	Coniferous	Clearcutting (10-20 y.a.): <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
46. Sullivan et al., 2008	British Columbia	Coniferous	Clearcutting: <i>M. gapperi</i> , <i>M. longicaudus</i> , <i>M. pennsylvanicus</i> , <i>P. maniculatus</i> , <i>S. cinereus</i> , <i>T. amoenus</i> ,
47. Swan et al., 1984	Nova Scotia	Deciduous	Clearcutting: <i>B. brevicauda</i> , <i>M. gapperi</i> , <i>M. pennsylvanicus</i> , <i>N. insignis</i> , <i>S. cinereus</i> . Partial harvest: <i>B. brevicauda</i> , <i>N. insignis</i> , <i>S. cinereus</i>
48. Von Trebra et al., 1998	British Columbia	Coniferous	Partial harvest: <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>T. amoenus</i> ,
49. Walters, 1991	British Columbia	Coniferous	Clearcutting (10-20 y.a.): <i>M. gapperi</i> , <i>P. maniculatus</i> , <i>S. cinereus</i>
50. Waters and Zabel, 1998	California	Coniferous	Partial harvest: <i>P. maniculatus</i> , <i>T. amoenus</i>
51. Zwolak and Foresman, 2007	Montana	Coniferous	Wildfire: <i>M. gapperi</i> , <i>P. maniculatus</i>
52. Zwolak 2008	Montana	Coniferous	Wildfire: <i>M. gapperi</i> , <i>P. maniculatus</i>

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**Appendix B.**—Highest-ranked models used to estimate survival and abundance of deer mice (*Peromyscus maniculatus*) in burned and unburned study sites.

Rank/Model	$K$	$\Delta_i AIC_c$	$w_i$
<b>2006</b>			
1 $\Phi, p, c_{M*B}$	8	0.00	0.234
2 $\Phi, p_B, c_{M*B}$	9	1.24	0.126
3 $\Phi_B, p, c_{M*B}$	9	1.78	0.096
4 $\Phi_M, p, c_{M*B}$	9	1.98	0.087
5 $\Phi, p, c_M$	5	2.40	0.071
6 $\Phi_B, p_B, c_{M*B}$	10	2.42	0.070
7 $\Phi_M, p_B, c_{M*B}$	10	3.26	0.046
8 $\Phi, p_M, c_{M*B}$	10	3.55	0.040
9 $\Phi, p_B, c_M$	6	3.62	0.038
10 $\Phi_B, p, c_M$	6	4.15	0.029
<b>2007</b>			
1 $\Phi, p_M, c_{M*B}$	10	0.00	0.494
2 $\Phi_B, p_M, c_{M*B}$	11	1.96	0.185
3 $\Phi_M, p_M, c_{M*B}$	11	1.97	0.185
4 $\Phi, p_{M*B}, c_{M*B}$	13	5.24	0.036
5 $\Phi_{M*B}, p_M, c_{M*B}$	13	5.97	0.025
6 $\Phi, p, c_{M*B}$	8	6.65	0.018
7 $\Phi_M, p_{M*B}, c_{M*B}$	14	7.22	0.014
8 $\Phi_B, p_{M*B}, c_{M*B}$	14	7.25	0.013
9 $\Phi_M, p, c_{M*B}$	9	8.36	0.008
10 $\Phi_B, p, c_{M*B}$	9	8.63	0.007

**Note:** Survival ( $\Phi$ ), probability of capture ( $p$ ), and probability of recapture ( $c$ ) were modeled as constant (no subscripts), differing among monthly trapping sessions (denoted with subscript  $M$ ), differing between burned and unburned sites (subscript  $B$ ), or changing both among trapping sessions and between burned and unburned sites (subscript  $M*B$ ). The models were run in program MARK and ranked according to  $\Delta AIC_c$ .  $K$  denotes the number of parameters and  $w_i$  can be interpreted as the weight of evidence in favor of model  $i$  (Burnham and Anderson 2002).