

# Deer mouse demography in burned and unburned forest: no evidence for source–sink dynamics

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**Abstract:** Deer mouse (*Peromyscus maniculatus* (Wagner, 1845)) populations increase dramatically after wildfires. 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 forests 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 mass, reproductive performance, or survival when compared with 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.

**Résumé :** Les populations de souris sylvestres (*Peromyscus maniculatus* (Wagner, 1845)) s'accroissent de façon considérable après un feu de brousse. Ces accroissements sont énigmatiques parce qu'il n'existe pas de source évidente de nourriture, ni de couverture végétale dans les régions ayant subi un feu important. Nous avons mené une étude de capture–marquage–recapture de souris sylvestres dans une mosaïque de forêts de montagne brûlées et intactes dans l'ouest du Montana afin de déterminer si l'accroissement qui suit le feu peut s'expliquer par une dynamique de type source–puits, dans laquelle les surfaces brûlées agissent comme puits. Lorsque les densités globales de souris sont très basses, la vaste majorité de la population se retrouve dans les zones brûlées. Les souris fréquentent régulièrement la forêt intacte seulement lorsque les densités sont fortes. Ce patron représente précisément l'inverse de la réaction attendue si l'hypothèse du puits est correcte. De plus, les souris dans les zones brûlées n'affichent pas de déclin dans leur masse corporelle, ni leur performance reproductrice, ni leur survie par comparaison aux souris des sites intacts. La structure en âges et le rapport mâles :femelles ne diffèrent pas entre les sites brûlés et intacts. Nous concluons que les zones incendiées n'agissent pas comme puits pour la population; au contraire, elles représentent un habitat de grande qualité pour les souris sylvestres.

[Traduit par la Rédaction]

## 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 fires, which often result 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; for exceptions see, e.g., Grinnell 1917; Levins 1969). Habitat-specific demogra-

phy 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; 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

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habitat selection of deer mice, *Peromyscus maniculatus* (Wagner, 1845), in burned and unburned montane forests. This species is renowned for its capability for spectacular increase in abundance after forest disturbances such as wild and prescribed fires (e.g., Halvorson 1982; Bock and Bock 1983; Martell 1984; Crête et al. 1995; Converse et al. 2006). These increases are puzzling for several reasons. First, there is no apparent food in severely burned areas. Second, severe fires often remove 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) and 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 abundances. 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 forests as a result of 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 a high-density sink

population being maintained by an influx of surplus individuals from a 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

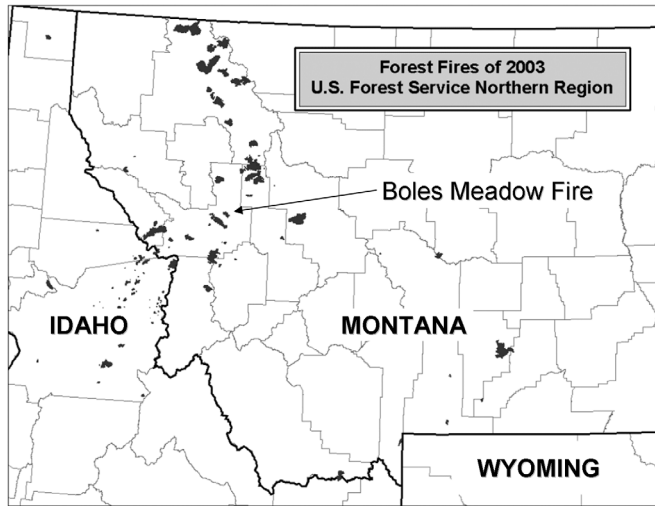
### Study site

The study was conducted at Boles Meadow (47°60'N, 113°45'W), located in the Seeley Valley, ~40 km northeast of Missoula, Montana (Fig. 1). The area was predominantly a Douglas-fir (*Pseudotsuga menziensis* (Mirbel) Franco) – western larch (*Larix occidentalis* Nutt.) forest. The understory was dominated by common beargrass (*Xerophyllum tenax* (Pursh) Nutt.) and huckleberry (genus *Vaccinium* L.). Boles Meadow burned in August 2003 in a lightning-strike-induced fire that encompassed 2000 ha of the forest. At the beginning of summer 2004, six trapping grids were constructed: two (C1 and C2) in unburned forest 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. Grids F1–F4 were located within a high-severity burn, where the fire killed all trees and completely removed the litter layer. During the 1st year after the fire, there was little to no understory vegetation in these trapping grids. In the 2nd year after the fire, the understory consisted mainly of fireweed (*Epilobium angustifolium* subsp. *angustifolium* L.) and heartleaf arnica (*Arnica cordifolia* Hook.) (for more detailed description of the effects of fire on vegetation see Zwolak and Foresman 2007). 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 >200 m from the edge of the burn patches and, in the case of grids F1–F4, from unburned patches within the burned area.

### 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 3 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 area and two burned areas. Sites within each set were trapped at the same time. In 2004, trapping at sites C1, F1, and F3 began 1 June and ended 6 August. At sites C2, F2, and F4, trapping began on

**Fig. 1.** Wildfires that burned in the area of western Montana in 2003 (modified from National Resource Information System, <http://nris.mt.gov> [accessed 4 October 2007]), with the study site indicated by an arrow.



8 June and ended 13 August in 2004. In 2005, the schedule was the same as in 2004, but trapping began and ended 1 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  $10 \times 10$  square with 10 m spacing between traps. To increase the number of captures and hence the precision of the population estimates, in 2005 the grids were enlarged to 144 trap stations ( $12 \times 12$  square). 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 the 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 sizes ( $AIC_c$ ) and ranked according to  $\Delta AIC_c$ . The model that fits the data best receives a  $\Delta AIC_c$  of 0. Models with  $\Delta AIC_c \leq 2$  have strong support, those with  $4 \geq \Delta AIC_c \geq 7$  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 (5 out of 241 individuals captured in 2004 and 4 out of 102 in 2005 moved among burned sites), each captured individual was assigned to a group according to the trapping site (6 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 day periods), capture ( $p$ ), and recapture ( $c$ ) probabilities were modeled as (i) constant, (ii) differing between burned and unburned sites, (iii) changing among primary periods, or (iv) 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): (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):  $M_{t+1} + \frac{f_0}{C}$ ,  $M_{t+1} + f_0 C$ , where  $C = \exp\left\{1.96\sqrt{\log\left[1 + \frac{\text{var}(\hat{N})}{f_0}\right]}\right\}$  and  $f_0 = \hat{N} - M_{t+1}$  are the numbers 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 the 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  $\hat{A}$  is the estimated area of a grid and  $L$  is the length of a 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 a 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 percentage of females and males captured in reproductively active condition in each primary period. Females were considered repro-



ductively 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™ 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 gray). This molt is usually finished by the 21st 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 mean 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 and 8 in unburned areas) 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 probabilities, 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 area; 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 (*Peromyscus maniculatus*) in burned and unburned forests in year 2004 and 2005.

Model					
$\Phi$	$p$	$c$	#P	$\Delta AIC_c$	$AIC_c$ weight
<b>2004</b>					
PP	(.)	PP×fire	12	0.000	0.557
PP	Fire	PP×fire	13	2.090	0.196
PP	PP	PP×fire	15	3.296	0.107
PP×fire	(.)	PP×fire	15	4.945	0.047
(.)	(.)	PP×fire	10	5.843	0.030
PP×fire	Fire	PP×fire	16	6.898	0.018
Fire	(.)	PP×fire	11	7.788	0.011
(.)	Fire	PP×fire	11	7.878	0.011
PP×fire	PP	PP×fire	18	8.353	0.009
(.)	PP	PP×fire	13	8.735	0.007
<b>2005</b>					
(.)	(.)	(.)	3	0.000	0.144
(.)	(.)	Fire	4	0.579	0.108
PP	(.)	(.)	5	0.914	0.091
Fire	(.)	(.)	4	0.950	0.090
PP	(.)	Fire	6	1.518	0.068
Fire	(.)	Fire	5	1.541	0.067
(.)	Fire	(.)	4	1.850	0.057
(.)	(.)	PP	6	1.980	0.054
(.)	Fire	Fire	5	2.441	0.043
PP	Fire	(.)	6	2.627	0.039

**Note:** Apparent survival ( $\Phi$ ), probability of capture ( $p$ ), and probability of recapture ( $c$ ) were modeled as constant (.), 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 Akaike's information criterion adjusted for small sample sizes ( $AIC_c$ ). #P is the number of parameters.

### MMDM and effective grid size

MMDM tended to decline throughout the summer, but not significantly so (linear regression:  $F_{[1,201]} = 2.316$ ,  $P = 0.103$ , slope (SE) =  $-2.782$  (1.828) for 2004 and  $F_{[1,113]} = 0.530$ ,  $P = 0.468$ , 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 to be 48.9 m (SE = 5.4 m), whereas the MMDM in burned areas was estimated to be 36.3 m (SE = 1.9 m). This difference was significant ( $t_{[215]} = 2.225$ ,  $P = 0.027$ ), 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 not significant ( $t_{[97]} = 1.024$ ,  $P = 0.308$ ) and we used one value of MMDM, 44.5 m (SE = 2.8 m), to calculate the effective grid size (3.79 ha).

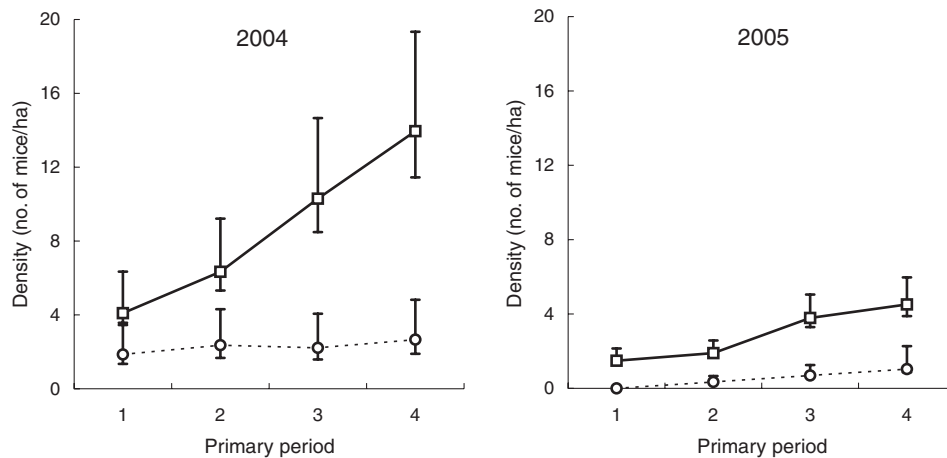
### Population density

Throughout the first summer after the fire, densities of mice in unburned areas remained relatively low ( $\sim 2$  mice/ha), 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 mean density of deer mice in burned areas was estimated to be 14.0 mice/ha (95% CI: 12.7–16.7 mice/ha), over five times higher than the mean density in unburned

**Table 2.** Model-averaged probability of capture ( $p$ ) and recapture ( $c$ ) of deer mice (*Peromyscus maniculatus*) in each primary period (1–4) during summer 2004 and 2005.

	Probability of capture ( $p$ )				Probability of recapture ( $c$ )			
	1	2	3	4	1	2	3	4
<b>2004</b>								
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)
<b>2005</b>								
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)

Note: Unconditional standard errors are in parenthesis.

**Fig. 2.** Changes in the mean density of deer mice (*Peromyscus maniculatus*) in burned (solid line) and unburned (broken line) forests during summer 2004 and 2005. The whiskers represent 95% CI of the estimates.

sites at the same time (2.7 mice/ha; 95% CI: 2.3–3.8 mice/ha). In 2005, mouse density was markedly lower both in burned and in 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, because of the low number of captures that year (particularly in unburned sites), survival estimates were characterized by large standard errors and the 95% CI overlapped widely.

For both sexes and both years, the proportion of reproductively active deer mice was higher in burned areas (Table 3). However, because of 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 was 20.1 g (SE = 0.60 g) in unburned areas and 19.5 g (SE = 0.24) in burned areas. This difference was not significant ( $t_{[199]} =$

0.944,  $P = 0.348$ ). Similarly, in 2005, the mean body mass in unburned (19.4 g, SE = 1.14 g) and burned (20.5 g, SE = 0.27 g) areas was not significantly different ( $t_{[54]} = 1.086$ ,  $P = 0.282$ ).

### Age structure and sex ratio

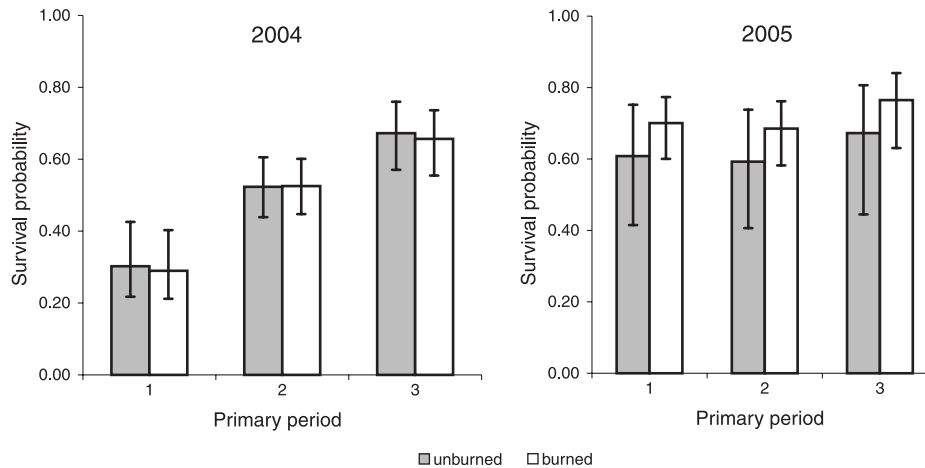
In 2004, the proportion of juveniles increased throughout the summer, ranging from 0.28 in June to 0.67 in August, but did not differ between burned and unburned areas (Fisher's exact test,  $P > 0.5$  in each primary session). In 2005, the number of individuals captured in unburned areas was too small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

### 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 (i) burned areas provide

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



**Table 3.** Percentage of reproductively active deer mice (*Peromyscus maniculatus*) in burned and unburned sites and *P* value for the difference (from Fisher's exact test).

Year	Sex	Burned sites		Unburned sites		<i>P</i>
		Percentage	<i>n</i>	Percentage	<i>n</i>	
2004	Female	53	62	40	15	0.40
	Male	51	51	20	10	0.09
2005	Female	32	21	0	1	1.00
	Male	72	79	40	5	0.15

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

highly suitable habitat for deer mice and (ii) 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 the Alberta badlands. He concluded that this distance does not exceed 140 m.

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 (first trapping session) or all but one (second 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 and 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 a 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 investigat-

ing this question in a different wildfire that occurred in 2005; our preliminary observations do not indicate increases in food sources such as insects and seeds (R. Zwolak, unpublished data).

Causes other than food resources may also contribute to the increase of deer mice after wildfires 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 et al. 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 (Zwolak and Foresman 2007), there was no relationship between CWD volume and deer mouse abundance at a given trapping grid.

Furthermore, fires may reduce interspecific competition because species such as red-backed voles (*Clethrionomys gapperi* (Vigors, 1830)) that are numerically dominant in undisturbed forest disappear after a fire (e.g., Zwolak and Foresman 2007). 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 the 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.

In conclusion, 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).

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