

Reduced ectoparasite loads of deer mice in burned forest: From fleas to trees?

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Abstract. We tested whether reduced parasite loads might contribute to high post-fire abundances of deer mice (*Peromyscus maniculatus*). We performed parasite examinations of 54 mice captured in burned forest in the area of Davis Fire (western Montana, USA), and 26 mice captured in nearby unburned forest. Mean abundance of ectoparasites (fleas, ticks, and lice) was lower in burned than in unburned forest. The difference was particularly pronounced for fleas, which were reduced by 70% in burned forest. Endoparasites (i.e., nematodes and cestodes) were unaffected. Mechanisms for the lower mean abundance of fleas in burned areas are not known, but might involve flea mortality in burrows during fire or decreased transmission, survival, or both in the post-fire environment. We propose several hypothetical pathways through which reduced ectoparasite loads could cause an increase in deer mouse abundance, such as improved health status or increased foraging efficiency of mice, both of which could translate into the increased reproduction that has been reported in mice from burned forest. We encourage experimental tests of the ectoparasite release hypothesis of the post-fire increase in deer mouse abundance.

Key words: disturbance; fleas; forest fire; Montana; parasite release; *Peromyscus maniculatus*; Rocky Mountains.

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INTRODUCTION

Determining ecological processes that shape the density and dynamics of vertebrate populations has been a long-standing objective in ecology. Traditionally, parasites were thought to be unlikely candidates for drivers of host population dynamics (Ostfeld 2008). However, recent experimental studies suggest that this view should be reevaluated. Endoparasites, acting independently (Vandegrift et al. 2008, Vandegrift and Hudson 2009) or in conjunction with other factors (e.g., behavioral changes or food availability: Mougeot et al. 2003, Pedersen

and Greives 2008), have been found to influence the abundance of species such as red grouse *Lagopus lagopus scoticus* (Hudson et al. 1998), Soay sheep *Ovis aries* (Wilson et al. 2004), reindeer *Rangifer tarandus* (Albon et al. 2002), and *Peromyscus* mice (Pedersen and Greives 2008, Vandegrift et al. 2008).

In contrast to endoparasites, population-level impacts of ectoparasites are largely unstudied, except for cases when they serve as disease vectors (e.g., of plague in prairie dogs: Wagner et al. 2006). On the other hand, there are multiple studies demonstrating individual-level impacts of ectoparasites on hosts, with most research

conducted on fleas. In laboratory studies, fleas were found to affect body condition, growth rate, life span, and energy expenditure of their hosts (e.g., Hawlena et al. 2006a, Devevey et al. 2008, Devevey and Christe 2009). In free-living animals, ectoparasites influenced host energy budgets (Giorgi et al. 2001, Nilsson 2003, Kam et al. 2010), litter size (Neuhaus 2003), foraging and vigilance patterns (Scantlebury et al. 2007, Raveh et al. 2011), and juvenile survival (Hawlena et al. 2006b). Such effects could translate into effects on host population abundance, but evidence for such impacts is lacking. Conventionally, this lack of evidence has been interpreted as an indication that ectoparasites do not affect host populations. Alternatively, this lack of evidence could reflect a lack of appropriate tests.

Deer mice (*Peromyscus maniculatus*) are generalist North American rodents known to increase in abundance after forest disturbances (Zwolak 2009). These increases are particularly pronounced after stand-replacement fires, with population densities in burned forest usually 2–5 times higher than in unburned forest (Krefting and Ahlgren 1974, Clough 1987, Crête et al. 1995, Kyle and Block 2000, Zwolak and Foresman 2008, Zwolak et al. 2012). High post-fire abundance of deer mice might affect other components of the ecosystem: as a prominent example, intense seed predation by deer mice prevents seedling establishment in burned forest (Zwolak et al. 2010). Because deer mice can hamper forest regeneration, and because fire frequencies in the western U.S. are increasing (Westerling et al. 2006), it is extremely important to determine why their population densities increase after fires. However, the specific causes of deer mouse increases in burned forest are still unclear.

In our previous research, we tested several obvious explanations for the deer mouse increase, such as source-sink dynamics, predatory release or increased food abundance in burned forest, but none of them was supported by data (Zwolak and Foresman 2008, Zwolak et al. 2012). Deer mice have similar survival and increased reproduction in burned vs. unburned forest, which suggests that burned forest is high quality habitat for deer mice and not a population sink (Zwolak and Foresman 2008, Zwolak et al. 2012). Food abundance appears similar or lower in burned than in unburned forest (Zwolak et al.

2012). Deer mouse survival did not differ between burned vs. unburned forest, which does not support release from predation as a mechanism of higher mouse abundance (Zwolak et al. 2012). We found that mice were more effective in foraging in burned than in unburned forest, but we did not identify the mechanism for the difference, although simplified habitat structure probably played a role (Zwolak et al. 2012).

In this study, we compare parasite loads of deer mice in burned and unburned forest as a possible alternative to the hypotheses we tested (and largely rejected) in the studies above. We were motivated by two major observations. First, several studies demonstrate that parasites negatively influence reproduction in rodents (Neuhaus 2003, Deter et al. 2007, Vandegrift et al. 2008, Hillegass et al. 2010), suggesting that a decrease in parasitism could explain the increase in mouse reproduction that we have observed in burned forest (Zwolak and Foresman 2008, Zwolak et al. 2012). Secondly, we also had reasons to suspect that fire could suppress parasite populations. Forest fires reduce arthropod abundances (for example, Orthoptera are less abundant one year after fire: Zwolak et al. 2012), and this could reduce levels of parasitism by both endoparasites and ectoparasites. Endoparasites with indirect life cycles (i.e., requiring multiple host species, in contrast to direct life cycles involving one host species) spend part of their life cycle in invertebrate hosts. For example, *Pterygodermatites peromysci*, a common nematode endoparasite of the white-footed mouse (*Peromyscus leucopus*) in the eastern USA (Vandegrift and Hudson 2009, Gear et al. 2012), requires an arthropod intermediate host (camel crickets, Orthoptera) to complete its life cycle (Luong and Hudson 2012). Furthermore, although some ectoparasites, such as lice, are permanent, and do not leave hosts except to disperse, others, such as fleas and ticks, are intermittent parasites, which may spend substantial time off their hosts, and these free-living stages may be reduced by forest fire. Thus, fire disturbance could create harsh abiotic conditions for ectoparasites off of their hosts, lower abundance of endoparasites' intermediate hosts, or both. Together, these observations suggested to us that fires could lead to lower endo- and ectoparasite survival, transmission, or both, with subsequent impacts on mouse

populations, and ultimately, cascading effects on seedling establishment, and forest regeneration (Zwolak et al. 2010).

METHODS

All materials and procedures were conducted according to an animal use protocol approved by the Western Illinois University Institutional Animal Care and Use Committee (27 May 2011).

Sampling mice

The deer mice were collected in west-central Montana, USA, in an area approximately 40 km north-west of the state capitol Helena. We trapped mice within and around the Davis Fire (46°52' N, 122°29' W, elevation approximately 2000 m.s.l.): an escaped prescribed fire that burned 815 ha of Douglas-fir (*Pseudotsuga menziesii*), lodgepole pine (*Pinus contorta*) and subalpine fir (*Abies lasiocarpa*) forest in August 2010.

The trapping was conducted from 9 July 2011 to 4 August 2011. In total, we trapped at 7 different sites: 2 in burned, and 5 in unburned forest, with trapping lasting 2–3 days per site. All sites were separated by at least 0.5 km. Traps at each site were located at least 100 m from the edge of the burn (in either burned or unburned habitat). At each site, we established 4–8 parallel trap lines located 20–40 m from one another. Each trap line contained 20–51 Victor traps placed at 10-m intervals. The traps were baited with peanut butter and marked with pin flags. Traps were set at approx. 19:00 and checked approx. 08:00 the next day. In total, the trapping effort equaled 1114 trap nights in burned forest and 3216 trap nights in unburned forest. The unequal trapping effort (i.e., numbers of sites and trap nights) was necessary due to low mouse densities in unburned forest (see *Results: Mouse captures*).

Collected mice were stored in individual Ziploc bags and placed in coolers filled with ice for 0.5 to 2.5 days (minimum and maximum time before transportation to the lab), and then frozen until necropsy. At dissection, host sex was determined and body mass was measured. Reproductive status of females (pregnant or not) was determined during dissections, based on the presence of embryos.

Parasite surveys

Hosts were examined for ectoparasites by ruffling their fur over a white dissection board. Ziploc bags, dissection boards, and hosts were then thoroughly examined with a 16× monocular loupe. Examination for endoparasites included visual inspection of the surface of the liver, and removal of the host's entire digestive tract. The stomach, small intestine, cecum, and large intestine were placed in individual Petri dishes under saline solution, split longitudinally, and then the fluid was decanted until clear enough for inspection with a dissecting microscope.

Preliminary parasite identification was performed at dissection. Ectoparasites and nematodes were stored in 70% ethanol, and cestodes in AFA (alcohol-formalin-acetic acid), for later identification of each individual. All parasites were identified to species (when possible) based on diagnostic anatomical features (list of used keys and original descriptions in Vaughn et al., *unpublished manuscript*). Non-tick mites were not identified to species due to their extremely high abundance and very small size.

Statistical analysis

We used parasite abundance (the number of parasites in a host: Bush et al. 1997) as an overall measure of parasitic infection. Abundance is a function of two commonly-reported measures of parasitism: prevalence (fraction of hosts infected) and mean intensity (mean number of parasites in infected hosts). We also analyzed prevalence and intensity separately, but this analysis did not reveal new patterns (see Appendix: Table A1). In order to test whether fire affected mouse infection by parasites, we analyzed mean parasite abundance with generalized linear mixed models (GLMMs; Paterson and Lello 2003) using Poisson family error terms, a log link function, and overdispersion included in the random effects models (described later in this section). The models were implemented via the lme4 package (Bates et al. 2011) in R (R Development Core Team 2012).

We conducted two separate analyses with parasite abundance as the response variable: one for all ectoparasites and the other for all endoparasites. Potential predictor variables included several fixed effects: burned vs. unburned forest (hereafter “burn”), male vs. female mice

(hereafter “sex”) and body mass (a continuous covariate, hereafter “mass”). We also included parasite taxon (hereafter “taxon”) as a fixed effect to test whether infection levels differed among parasites. In the case of ectoparasites, taxon included three categories: lice, fleas, and ticks. In the analysis of mean endoparasite abundance, taxon had two categories: nematodes and cestodes. Due to low frequencies of individual parasite species (all infested fewer than 30% of hosts, and most infested <10% of hosts) different species within each category were pooled together.

Random effects included a unique identifier for each observation, i.e., for each parasite taxon within each mouse; this procedure is identical to using an overdispersed Poisson model. Including a random effect of trapping site, or modifying the random effect structure to include partly correlated variances across individual mice or sites, did not improve fit, and these effects were not included in the final models (unpublished analyses).

The initial, full model included all possible interactions among the fixed effects. The final structure of the models was determined through backward stepwise elimination of non-significant interactions using likelihood ratio tests.

RESULTS

Mouse captures

In total, we captured 81 deer mice: 55 in the burned forest (trap success of 4.94 captures per 100 trap nights) and 26 in unburned forest (0.81 captures per 100 trap nights). All the mice except one (from burned forest) were collected and examined for parasites. Sex ratio of collected mice did not differ between burned and unburned forest (Fisher exact test, $P = 0.24$). Among adult females (body mass greater than 15 g, $n = 16$ for burned forest and 10 for unburned forest), more were found pregnant in burned than in unburned forest (50% vs. 30%), but the difference was not significant (Fisher exact test, $P = 0.43$). The trapping also yielded southern red-backed voles (*Myodes gapperi*), western heather voles (*Phenacomys intermedius*), chipmunks (*Tamias* spp.), northern pocket gophers (*Thomomys talpoides*), and shrews (*Sorex* spp.).

Ectoparasites

We found 14 ectoparasite taxa (10 species of fleas, 2 species of lice, and 2 species of ticks) on the collected deer mice (Table 1). The ectoparasite taxa varied in abundance (taxon effect in Table 2a), with fleas being most abundant, followed by lice, and then by ticks (Table 3a). Ectoparasites were less abundant on mice captured in burned than in unburned forest (burn effect in Table 2a), although the influence of fire on abundance appeared to vary in strength among ectoparasite taxa (burn \times taxon effect in Table 2a). The reductions in abundance in burned relative to unburned forest were pronounced in fleas and ticks but not in lice (Table 3a). In addition, male hosts had more ectoparasites than females (sex effect in Table 2a). Finally, the relationship between deer mouse body mass and parasite loads differed among ectoparasite taxa: fleas tended to be more common on heavy mice, lice tended to be less common on heavy mice, and tick numbers were unaffected by host body mass (mass \times taxon effect, Table 2a).

Endoparasites

We found at least 8 endoparasite taxa (6 nematode species, and 2 cestode species, plus several unidentifiable nematodes) in the collected mice (Table 1). The nematode *Calodium hepaticum* was excluded from our analysis because infection consists of eggs deposited throughout the liver (Spratt and Singleton 1986), and it is not feasible to count individual worms. The estimated mean abundance of nematodes was marginally higher than that of cestodes (taxon effect in Table 2b). Other predictor variables did not influence endoparasite abundance in captured mice (non-significant effects of burn, sex, and mass in Table 2b; see also abundance estimates in Table 3b).

DISCUSSION

Our trapping results (trap success over 6 \times higher in the burned than in the unburned forest) corroborate past evidence of higher mouse densities in burned forest (Zwolak 2009, Zwolak et al. 2012) and the parasite surveys indicate that mice in burned forest are characterized by decreased abundance of ectoparasites. Could the lowered ectoparasite loads serve as a mechanism for this deer mouse population increase?

Table 1. Parasites found in deer mice *Peromyscus maniculatus* captured in burned and unburned forest in the area of Davis Fire, Montana, USA.

Taxon	Site on/in host	Life cycle†	Individuals collected
Arthropoda			
Fleas (Insecta, Siphonaptera)			
<i>Opisodasys keeni</i>	fur	intermittent	33
<i>Aetheca wagneri</i>	fur	intermittent	31
<i>Catallagia decipiens</i>	fur	intermittent	4
<i>Megabothris abantis</i>	fur	intermittent	3
<i>Peromyscopsylla selenis</i>	fur	intermittent	3
<i>Amaradix euphorbi</i>	fur	intermittent	2
<i>Peromyscopsylla hesperomys</i>	fur	intermittent	2
<i>Epitedia wenmanni</i>	fur	intermittent	1
<i>Malaraeus telchinus</i>	fur	intermittent	1
<i>Rhadinopsylla fraterna</i>	fur	intermittent	1
Unknown flea	fur	intermittent	2
Lice (Insecta, Anoplura)			
<i>Polyplax auricularis</i>	fur	permanent	44
<i>Hoplopleura hesperomydis</i>	fur	permanent	19
Ticks (Acarina, Ixodida)			
<i>Dermacentor andersoni</i>	skin	intermittent	11
<i>Ixodes angustus</i>	skin	intermittent	1
Nematoda			
<i>Syphacia peromysci</i>	cecum	direct	1884
<i>Heligmosomoides vandegrifti</i>	small intestine	direct	135
<i>Aspiculuris americana</i>	large intestine	direct	35
<i>Physaloptera</i> sp.	large intestine	indirect	2
<i>Protospirura numidica</i>	stomach	indirect	1
<i>Calodium hepaticum</i>	liver	direct	n/a
Unknown nematode	stomach/small intestine/large intestine	unknown	5
Eucestoda			
<i>Choanotaenia peromysci</i>	small intestine	indirect	57
<i>Hymenolepis</i> sp.	small intestine	indirect	10

†Permanent ectoparasites do not leave hosts except to disperse; intermittent ectoparasites may spend substantial time off their hosts. Endoparasites with indirect life cycles require multiple host species; direct life cycles involve one host species.

There is growing evidence that ectoparasites contribute to high post-fire deer mouse abundance, e.g., through effects on body condition (Hawlena et al. 2006a, Devevey et al. 2008, Devevey and Christe 2009) or feeding behavior (Scantlebury et al. 2007, Raveh et al. 2011), which in turn influences reproductive output of deer mice. Intriguingly, Raveh et al. (2011) showed that flea-infested rodents were less vigilant and

Table 2. Factors influencing (a) ectoparasite and (b) endoparasite abundance in deer mice *Peromyscus maniculatus*.

Variable†	χ^2	df	P
(a) Ectoparasites			
Burn	8.02	1	0.005
Sex	12.64	1	<0.001
Mass	0.11	1	0.745
Taxon	24.08	2	<0.001
Burn × Taxon	5.78	2	0.056
Mass × Taxon	5.68	2	0.058
(b) Endoparasites			
Burn	0.44	1	0.507
Sex	0.06	1	0.806
Mass	0.72	1	0.396
Taxon	3.99	1	0.046

†Burn indicates burned vs. unburned forest; sex denotes sex of the host; mass denotes host body mass; taxon indicates parasite taxon. See *Methods: Data analysis* for further explanation.

Table 3. Estimated average abundance of parasites on deer mice *Peromyscus maniculatus* captured in the area of Davis Fire, Montana, with 95% confidence intervals presented in parentheses.

Taxon	Unburned forest	Burned forest
(a) Ectoparasites		
Fleas	0.686 (0.311–1.510)	0.205 (0.102–0.413)
Lice	0.152 (0.051–0.453)	0.213 (0.106–0.426)
Ticks	0.110 (0.033–0.361)	0.012 (0.001–0.109)
(b) Endoparasites		
Cestodes	0.002 (0.000–0.366)	0.001 (0.000–0.150)
Nematodes	0.012 (0.000–0.304)	0.007 (0.001–0.084)

had higher giving-up densities (i.e., tended to quit foraging at higher densities of food remaining in the patch). In our previous research (Zwolak et al. 2012), we found that deer mice in unburned forest had higher giving-up densities than mice from burned forest, but the reason for this difference was unclear. Results of this study suggest that lower flea abundance could provide a mechanism for the increased foraging success of mice in burned forest (flea-free mice have lower giving-up densities, thus are more efficient foragers), acting jointly with the fire-related simplification of habitat structure that increased food encounter rates (Zwolak et al. 2012). As we suggested in our previous work (Zwolak et al. 2012), a higher rate of resource acquisition could translate into more intense reproduction observed in deer mouse populations inhabiting burned forest (Zwolak and Foresman 2008, Zwolak et al. 2012).

A separate but not mutually exclusive mechanism through which ectoparasites could suppress deer mouse abundance could be through their role as pathogen vectors (Azad et al. 1997, Jardine et al. 2006, Watkins et al. 2006). Evaluating this notion is not feasible with this data set. However, additional research consisting of analyses of blood samples of mice from burned and unburned forest could be a profitable area for future research.

Fleas appeared particularly affected by fire: their estimated average abundance in burned forest was reduced by 70% relative to that for mice from unburned forest. Why would forest fires affect flea loads in deer mice? As far as we know, there is no research on this topic (this is certainly a gap in current life-history knowledge), thus we offer three lines of speculation below.

First, fleas might die in burrows during forest fires. Deer mice usually nest in burrows below ground, inhabited also by their fleas. In most

cases, entire larval and pupal development of fleas takes place off-host, in burrows, and these stages may make up >90% of the flea population (Beck and Pfister 2004). The temperature and relative humidity within burrows are among the main factors determining flea development and survival, with immature stages being particularly susceptible to mortality caused by high temperature or low humidity (Marshall 1981, Rust and Dryden 1997, Krasnov et al. 2001, Osacar-Jimenez et al. 2001). Burrows of deer mice are rather shallow: Laundré and Reynolds (1993) report mean maximum depth of 19 cm (SD = 9 cm, $n = 26$), whereas forest fires can generate temperatures exceeding 50°C at soil depths of 50 cm and temperatures exceeding 75°C at 30 cm soil depth (Massman and Frank 2004: Fig. 1). Thus, fires could generate deadly temperatures in burrows. Additionally, fires might reduce oxygen concentration to lethal levels in burrows. Interestingly, if fire directly kills animals in burrows, it has opposing effects on the abundance of mice and their flea loads. Either deer mice are less susceptible to high temperatures and anoxia than their fleas, or mice have higher capability to quickly rebuild their populations in burned areas, with the response of fleas lagging behind.

Second, it is also possible that deer mouse flea populations are affected by the post-fire changes in entire small mammal communities, if flea numbers depend on the availability of a variety of hosts. Unlike deer mice, most small mammal species decrease in abundance after forest fires, and the declines are particularly drastic in red-backed voles, a species that is often numerically dominant in unburned forest (Zwolak and Foresman 2007, Zwolak 2009). However, the observed pattern of lower abundances of fleas in burned forest on deer mice was driven by declines in two flea species that were found typically on deer

mice (*Aetheca wagneri* and *Opisodasys keeni*; Table 1), not by fleas that were common on red-backed voles (Vaughn et al., *unpublished manuscript*). Therefore, a reduction in vole numbers is an unlikely explanation for the decrease in mouse fleas.

Finally, although we interpret our data to suggest that fires reduce flea infections, and that this leads to an increase in mouse population size, we acknowledge that the same patterns would result if causality were reversed. That is, it is possible that after fires, mouse numbers increase for reasons other than ectoparasite release, and that the reduction in flea loads reflects a “dilution” of fleas among hosts that became more abundant. If deer mouse increase is unrelated to their parasites loads, and the rates of reproduction and dispersal of deer mice exceed flea reproduction and transmission rates (Krasnov et al. 2002), average flea abundance would be lower in burned than in unburned forest simply due to a mismatch in host and parasite population dynamics. Such a phenomenon would be rather unexpected because both theoretical models and empirical data suggest positive correlations between average parasite abundance and host density (e.g., Anderson and May 1978, Arneberg et al. 1998). Therefore, more work is necessary to critically evaluate this idea.

As a caveat, the lower flea loads in burned vs. unburned forest were not our a priori expectation (initially, our focus was on endoparasites), thus these findings and their post-facto interpretation should be treated with caution (Mentis 1988). Furthermore, collecting fleas from snap-trapped mice could underestimate flea loads because some fleas could leave their dead host. However, we know of no reason why this would create a bias towards lower flea loads in burned vs. unburned forest (that is, no reason to suspect that mice from burned forest were consistently dead for a longer time before collection, or that fleas leave dead hosts more quickly in burned forest). In fact, non-directional measurement error caused by fleas leaving dead hosts would weaken the observed relationship between habitat and flea loads.

Mean abundance of ticks was also lower in the burned than in the unburned sites. Declines in tick abundance have often been reported after

prescribed forest fires (Jacobson and Hurst 1979, Stafford et al. 1998) and are usually explained by changes in temperature and humidity regimes and by destruction of litter cover (Stafford et al. 1998, Allan 2009). The abundance of ticks in areas burned by prescribed fires recovers within a year or two (Stafford et al. 1998, Allan 2009), thus the post-fire tick release is probably ephemeral. On the other hand, wildfires usually burn with much greater intensity than prescribed fires, hence the recovery of tick populations after forest fires might be slower than described in prescribed burn studies.

Although we detected main effects of fire on all ectoparasites, population-level effects on mouse abundance are most likely to be due to fleas. In other studies, the impact of ticks on small mammals appears minor. Although some studies show negative effects of tick infestation on their hosts (Pfäffle et al. 2009), others do not (Ostfeld et al. 1996). However, it is possible that the reduction in flea and tick abundance produces synergistic effects on deer mice. Lice appeared unaffected by forest fire. This finding is not surprising, given that lice spend their entire life cycle on the body of the host (Johnson et al. 2004), thus are less exposed to post-fire changes in environmental conditions than are fleas or ticks. Very little is known about the effect of louse infestation in small mammals. Lehmann (1992) did not detect adverse effects of lice on their gerbil (*Gerbillus andersoni*) hosts. On the other hand, studies conducted on birds demonstrated negative impact of lice on thermoregulation and metabolic rates (Booth et al. 1993).

We expected that drastic changes in environmental conditions associated with forest fires would reduce endoparasite loads in deer mice. Such an effect was indeed found in red-backed voles, *Myodes gapperi* (Hwang et al. 2010), a species which strongly declines after forest fires (Zwolak 2009). However, we did not detect a difference in endoparasite abundance between deer mice captured in burned and unburned forest. Thus, there is no evidence that the increased post-fire abundance of deer mice is caused by changes in their endoparasite loads.

Conclusions

We found that the abundance of ectoparasites on deer mice is reduced in burned forest. In

particular, flea abundance in deer mice in burned forest was several times lower than the abundance in unburned forest. Combined with our past research, these results lead to an unexpected hypothesis about the role of parasites in forest regeneration after fire: our past work has shown that mouse populations can be dramatically higher after wildfires (Zwolak and Foresman 2008, Zwolak et al. 2012), and that mouse predation of seeds suppresses seedling establishment (Zwolak et al. 2010). If the high mouse densities after forest fires are due to the reduced flea loads we have documented here, then the limiting factor for forest regeneration is the time required for flea populations to re-establish after burns. This hypothesis is correlational, and experimental manipulations, such as flea removal in unburned forest, introduction of flea-infected mice to burned forest, or both, would be required to test it. Although we are not planning further work in this system, we hope that this paper will encourage others to investigate this intriguing possibility in the future.

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SUPPLEMENTAL MATERIAL

APPENDIX

Table A1. Factors influencing intensity and prevalence of (a) ectoparasites and (b) endoparasites in deer mice *Peromyscus maniculatus* captured in the area of Davis Fire, Montana.

Variable†	Intensity			Prevalence		
	χ^2	df	P	χ^2	df	P
a) Ectoparasites						
Burn	<0.01	1	>0.999	12.05	1	<0.001
Sex	8.37	2	0.004	8.09	1	0.004
Mass	0.42	1	0.515	0.03	1	0.864
Taxon	3.67	2	0.159	27.33	2	<0.001
Burn × Taxon	6.60	2	0.037
Mass × Taxon	6.36	2	0.042
b) Endoparasites						
Burn	<0.01	1	0.996	1.28	1	0.257
Sex	<0.01	1	0.945	0.24	1	0.620
Mass	1.17	1	0.280	2.27	1	0.132
Taxon	0.19	1	0.659	16.96	2	<0.001
Burn × Sex	3.77	1	0.052

†Burn indicates burned vs. unburned forest; sex denotes sex of the host; mass denotes host body mass; taxon indicates parasite taxon. See *Methods: Data analysis* for further explanation.