

RESPONSES OF ENDOPARASITES IN RED-BACKED VOLES (*MYODES GAPPERI*) TO NATURAL FOREST FIRES

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ABSTRACT: We investigated the responses of endoparasites in red-backed voles (*Myodes gapperi*) to fire in a boreal forest ecosystem. Because fire affects the environmental conditions and biodiversity of the forest ecosystem, the life cycle of parasites may also be affected because of the absence of intermediate hosts in the environment. We hypothesized that the prevalence of endoparasites would be influenced by the parasites' life cycle and habitat characteristics (forest vs. burned). We found that prevalence of endoparasites was different between forested and burned habitats ($\chi^2=37.49$, $P<0.001$). Cestodes, nematodes, and coccidia showed different responses to habitat alteration ($\chi^2=37.43$, $P<0.001$). There was a higher prevalence of cestodes in forested (53.5%) than burned habitats (35.0%). However, there was higher prevalence of coccidia in burned (55.0%) than forested (42.9%) habitats. Furthermore, although prevalence of cestode infection was lower in burned than forested habitat, individuals in both habitats had similar intensities of cestodes. Our study showed that habitat can significantly affect the parasite communities, depending on specific parasite life cycles.

Key words: Cestodes, coccidia, forest fire, *Myodes gapperi*, nematodes.

INTRODUCTION

Parasite communities are influenced by many factors, including host specificity and ecologic characteristics of the host such as population size, habitat, diet, dispersal, and host immune defenses (Poulin and Morand, 2004). Because parasites exploit their host both as a food resource and as a habitat, their survival is dependent on the host's survival. Some have intricate life cycles, often involving one or more intermediate hosts. Temporal persistence of parasites with complex life cycles in an ecosystem depends not only on the survival and distribution of the definitive host, but also on the intermediate host communities, and environmental conditions (Poulin and Morand, 2004). At the host population level, intrinsic factors such as host age and sex influence parasite species in mammals (Pawelczyk et al., 2004; Krasnov et al., 2005). However, there may be considerable variability in parasite communities among different populations of the same host species.

The role of habitat and host density in altering parasite communities through time has been documented in some host-parasite systems (Forrester et al., 1987; Calvete et al., 2004; Torres et al., 2006) and Gardner and Campbell (1992) suggested that some mammal-parasite ecologic communities can persist over time scales discoverable only using phylogenetic-historical ecologic methods (sensu Brooks, 1985). Despite the fact that much work has been conducted on parasite communities, little effort has been focused on the effects of ecologic disturbances at the level of the parasite community.

Small-mammal responses to fire have been studied in prairie savannah (Beck and Vogl, 1972) and Mediterranean ecosystems (Haim et al., 1996; Torre and Díaz, 2004) that experience frequent wildfires. However, small-mammal responses to fire in temperate boreal ecosystems have been rarely documented. Also, to our knowledge the relationship between endoparasites and small mammals recovering after a forest fire has not

been examined. In general, small-mammal communities appear to recover rapidly after fire, matching successional changes in vegetation structure (Haim and Izhaki, 2000). Because fire affects the environmental conditions and biodiversity of the forest ecosystem, the life cycle of parasites may also be affected because of the absence of intermediate hosts in the environment. Thus, even if the definitive host is able to recolonize the burned habitat, the parasites may not be able to complete their life cycle in the altered environment.

In 2003, 17,000 acres of boreal forest was burned in Kootenay National Park, British Columbia, Canada (50°68'N, 115°93'W). We hypothesized that the prevalence of endoparasites in red-backed voles (*Myodes gapperi*) would be influenced by the parasites' life cycle and habitat type (i.e., intact forest vs. burn). We predicted that there would be a similar prevalence of endoparasites that have direct life cycles, such as nematodes and coccidia, between burned and intact forest, whereas the prevalence of cestodes, which have an indirect life cycle, would be higher in the intact forest than in the burned forest.

MATERIALS AND METHODS

Sixty-three (37 male, 26 female) red-backed voles were live-trapped at Kootenay National Park in 2005 and 2006 using Longworth™ traps (Rogers Manufacturing, Peaceland, British Columbia, Canada) baited with sunflower seeds. Because of the seasonality of endoparasitic infection in the host, we collected samples during the same time period (22 July to 21 August) in both years. Animals were captured in intact forest and in burned habitats at least 1,000 m from intact forest. We captured 43 voles in the forested habitat and 20 voles in the burned habitat. Because red-backed voles have a high affinity for coniferous forest, they showed limited ability to recolonize early postburn communities (Beck and Vogl, 1972). Thus, we were limited to a smaller sample of red-backed voles in the burned habitat.

We determined the body mass, sex, and age class of captured voles. Subsequently, they

were euthanized using CO₂ inhalation and examined for endoparasites. Lungs, liver, stomach, small intestine, cecum, large intestine, and bladder were examined for cestodes and nematodes. Feces were collected from the colon and preserved in 2% potassium dichromate (K₂Cr₂O₇) for further analysis of coccidia infection. Cestodes were killed in fresh or distilled water and fixed in 70% ethanol. For identification, they were stained with Semichon's acetic-carmin solution, dehydrated in ethanol, cleared in terpineol or xylene, and mounted in Damar gum. Nematodes were killed in glacial acetic acid and fixed in 70% ethanol. For identification, small nematodes were cleared in 3% glycerine-ethanol solution. Large nematodes were cleared in lactophenol. Sporulated coccidia oocysts were separated from the feces-dichromate mixture using a suspension of aliquot (1–3 ml) from the sample in 12 ml of modified Sheather's sugar flotation solution via centrifugation. Sporulated oocysts were then identified using light microscopy under an oil immersion objective. Representative specimens of parasites have been deposited in the Harold W. Manter Laboratory (HWML) of Parasitology, Lincoln, Nebraska, USA (HWML numbers 48382, 48385, and 48387–48393).

Prevalence of cestodes, nematodes, and coccidia in red-backed voles was compared among host sex, age, and habitat (forest vs. burn) using a three-dimensional chi-squared contingency table. Because helminth infections in mammals are often concentrated in only a few host individuals causing an overdispersion of data, we performed rank transformation on our data before using parametric analyses (Canover and Iman, 1981). Intensity of helminth infection was examined among host sex, age, and habitat using multi-factor analysis of variance (ANOVA). Body mass of red-backed voles was compared among sex, age, and habitat using a multi-factor ANOVA. The terms prevalence, intensity, mean intensity, and abundance follow the definitions of Margolis et al. (1982). All values represent mean ± SD.

RESULTS

We did not find significant differences in prevalence of cestodes ($\chi^2=2.56$, $P=0.20$), nematodes ($\chi^2=2.65$, $P=0.10$), or coccidia ($\chi^2=1.24$, $P=0.25$) between years. Thus, for the remaining analyses, we pooled the data for 2005 and 2006. We found no significant differences in body mass be-

TABLE 1. Prevalences, intensities, and abundances of helminthes and coccidia of 63 red-backed voles (*Myodes gapperi*) in Kootenay National Park, British Columbia, Canada.^a

	Site in host	Prevalence		Intensity		Abundance	
		No. infected	%	Mean±SE	Range	Mean±SE	Total individuals
Cestoda							
<i>Arostrilepis horrida</i>	SI	29	46	2.3±0.4	1–9	1.1±0.2	67
<i>Catenotaenia peromysci</i>	SI	1	2	NA	1–2	0.03±0.03	2
Nematoda							
<i>Mastophorus muris</i>	S	1	2	NA	1	0.16±0.16	1
<i>Syphacia petrusewiczii</i>	C	2	3	5.0±2.5	7–8	0.24±0.17	15
Coccidia							
<i>Eimeria</i> sp.	F	4	6	ND	ND	ND	ND
<i>Eimeria wenrichi</i>	F	21	33	ND	ND	ND	ND
<i>Isospora mcdowellii</i>	F	3	5	ND	ND	ND	ND

^a C = cecum; SI = small intestine; S = stomach; F = feces; NA = not applicable; ND = not determined.

tween males (20.8±0.59 g) and females (21.6±0.73 g; $F_{1,54}=0.71$, $P=0.40$) or between burned (20.6±0.76 g) and forested habitat (21.9±0.55 g; $F_{1,54}=1.84$, $P=0.18$). There were no significant interactions among sex, age, and habitat on body mass of voles ($P>0.20$).

We identified two species of cestodes, *Arostrilepis horrida* (syn. *Hymenolepis horrida*) and *Catenotaenia peromysci*, in the small intestine (Hwang et al., 2007). We found two species of nematodes, *Mastophorus muris* (in the stomach) and *Syphacia petrusewiczii* (in the cecum), in adult voles. Three species of coccidia were also found: *Eimeria* sp., *Eimeria wenrichi*, and *Isospora mcdowellii* (see Table 1).

Prevalence of cestodes was similar among host sex and age ($\chi^2=6.95$, $P>0.10$). We found nematodes only in adult red-backed voles, and there was no difference in prevalence of nematodes between host sexes ($\chi^2=2.61$, $P>0.50$). Prevalence of coccidia was also similar among host sex and age ($\chi^2=5.88$, $P>0.10$). Because we did not find any significant differences in the prevalence of endoparasites in host sex and age categories, for further analysis of habitat, we pooled host sex and age categories.

Prevalence of endoparasites was different between forested and burned habitats

($\chi^2=37.49$, $P<0.001$). Different endoparasitic groups (cestodes, nematodes, and coccidia) showed different responses to habitat alteration ($\chi^2=7.43$, $P<0.001$). For cestodes, there was a higher prevalence in forested (53.5%) than burned habitats (35.0%). However, for coccidia, there was higher prevalence in burned (55.0%) than forested (42.9%) habitats (Fig. 1).

Because of the low infection by nematodes, we excluded comparisons of nematode intensity among host sex, age, and habitat. Cestode intensity was related to host sex ($F_{1,23}=7.01$, $P=0.014$); males had 1.9±0.44 individuals, whereas females had 4.9±0.60 individuals. There was a significant interaction between host sex and age in cestode intensity ($F_{1,23}=12.149$, $P=0.002$). Infected adult female voles had 1.3±0.53 individuals, compared to 6.75±0.85 for juvenile females. In contrast, adult males had 2.9±0.41 individuals compared to 1.0±0.78 for juvenile males. There was no significant difference in infection intensity between voles in forested and burned habitat ($F_{1,23}=0.079$, $P=0.78$).

DISCUSSION

Overall, the prevalence of endoparasite groups that have indirect life cycles was

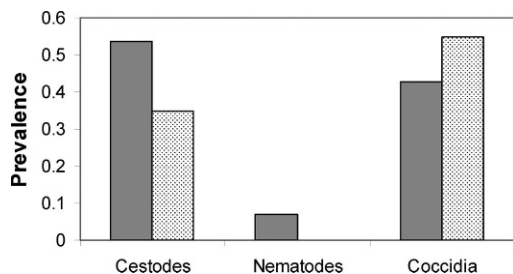


FIGURE 1. Prevalence of endoparasites in red-backed voles (*Myodes gapperi*; $n=63$) in forest (solid gray) and burned (stippled) habitats at Kootenay National Park, British Columbia, Canada, 2005–06.

lower in burned habitat than forest, and those with direct life cycles were most prevalent in burned habitat. We conclude that parasite communities were influenced not only by host characteristics, but also by habitat characteristics. The life cycles of cestodes are indirect; at least one intermediate host is required. Although the intermediate hosts of cestodes of voles in the Canadian Rockies are unknown, we assume that they are similar to those of closely related cestodes in other areas. For example, *Hymenolepis diminuta* requires an intermediate host, which is commonly a beetle (*Tenebrio molitor*) of the family Tenebrionidae, to complete its life cycle (Gardner and Schmidt, 1988). The intermediate hosts of *Catenotaenia pusilla* may be beetles, fleas, or free-living mites (Joyeux and Baer, 1945). Thus, we speculate that there may be an intermediate arthropod host involved in the life cycles for both *A. horrida* and *C. peromysci*. However, because of the limited recolonization of ground-dwelling arthropods in postburn habitat (Coleman and Rieske, 2006; Moretti et al., 2006), the arthropod diversity in these areas was probably severely reduced after the forest fire. Even though the recolonizing red-backed voles in burned habitat harbored a similar parasite intensity as those in forest, the parasite was not able to persist in burned habitat, as shown by the lower prevalence of cestodes in burned than intact forest. The intermediate host density and distri-

bution can significantly affect the parasite communities (Haukisalmi et al., 1987). This finding is similar to that of Forrester et al. (1987) who showed that agricultural practices such as harvesting and burning had a pronounced effect on the distribution of core helminth species of round-tailed muskrats (*Neofiber alleni*) in southern Florida.

Conversely, coccidia oocysts, such as those of *Eimeria* spp. survive and sporulate in the external environment and only then become infective to the host. Moisture, temperature, and direct sunlight may influence the sporulation of oocysts in the external environment, but the interactions of these factors are not well understood. In general, oocysts sporulate more rapidly at higher temperatures; exposure to temperatures less than 10 C or greater than 50 C is lethal to unsporulated oocysts (Duszynski and Upton, 2001). Thus, with the exposed ground cover in the burned habitat, the ground temperature would be higher in burned than in the intact forest habitat. Perhaps this leads to higher sporulation percentage and thus, increased transmission of coccidia oocysts, ultimately resulting in higher prevalence of coccidia in burned habitat. Similarly, the majority of the nematodes in voles have direct life cycles. In *Syphacia*, the embryonated eggs are directly infectious to voles (Lewis, 1987). The persistence of nematodes is highly related to the high transmission efficiency and long life span of the parasites (Haukisalmi et al., 1996). Furthermore, it has been documented that stochastic variation in temperature accelerates embryonation and development of the nematode egg even when mean temperatures remain the same (Saunders et al., 2002). However, we found very few red-backed voles infected with nematodes and could not examine this relationship further.

We did not find significant differences in the intensity of cestode infection in voles from the forested and burned habitat; this may be caused by the small

number of voles sampled in the burned habitat. However, we did not find any differences in body mass of voles in the burned and forested habitat, which implies that individuals in the burned habitat were not in poorer condition than those in the forested habitat. Often, the effects of parasitism on the recovery of animal communities have been neglected in ecosystem research. By using parasite communities as indicators of areas of high biologic and ecologic diversity (Gardner and Campbell, 1992), we can gain additional understanding of the functioning and recovery of disturbed ecosystem.

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