Small mammal communities after two recent fires in Yellowstone National Park
by Marilyn Anita Wood

A thesis submitted in partial fulfillment of the requirements for the degree of MASTER OF SCIENCE in Zoology
Montana State University

Abstract:
The small mammals, their food habits, and their food resources were studied during the summers of 1978 and 1979 on two burns and two adjacent spruce-fir, lodgepole pine forest sites in Yellowstone National Park. The Divide site burned in 1976, and the Trail Creek site burned in 1974. A study plot was established in each burn and control site, and the small mammals were sampled by snap-trapping and pitfall traps twice each summer. Stomach contents were analyzed. Quantitative data were obtained on plant coverage, concealment cover (measured by a coverboard), arthropod diversity and soil seed and fungal sclerotia numbers.

The plant communities were more diverse in control than burn sites and more diverse in the Trail Creek than the Divide sites. Tree and shrub coverage and log concealment were greater in the controls than their respective burns. The amount of bare ground was greater in the Divide Bum than any other site. No differences in forb and graminoid coverage and vegetative concealment were found between either bum and control sites. No differences between the burns and controls were found in numbers of either plant seeds or fungal sclerotia (Cenooooooion geophilum) recovered from the top 5 cm of the soil samples. Total arthropod numbers in the burn sites were similar to their respective control sites, but the burns supported larger numbers of dipterans and fewer araneidans and acarinans than the controls.

Ten species of small mammals were collected in the study areas. Clethrionomys gapperi was the most abundant small mammal in all_four sites, and fungi were the most important items in their diets (X range 77-98% relative density in all four sites). Peromysous maniculatus were more numerous in the bum sites than in the control sites, and arthropods were the most important item in all sites (X range 52-92%). Eutcamias amoenus were more numerous in the burns than in the controls and exhibited a large amount of individual variation in food habits. Arthropods, seeds, fungi, and forbs were all important in their diets. The hypothesis that numbers of Peromyscus maniculatus in the bums were limited by competition with Clethrionomys gapperi was tested by removal of Clethrionomys gapperi from two 0.36 ha plots in the Divide Burn; numbers of Peromysous maniculatis were not affected.

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IN YELLOWSTONE NATIONAL PARK

by

Marilyn Anita Wood

A thesis submitted in partial fulfillment
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ABSTRACT

The small mammals, their food habits, and their food resources were studied during the summers of 1978 and 1979 on two burns and two adjacent spruce-fir, lodgepole pine forest sites in Yellowstone National Park. The Divide site burned in 1976, and the Trail Creek site burned in 1974. A study plot was established in each burn and control site, and the small mammals were sampled by snap-trapping and pitfall traps twice each summer. Stomach contents were analyzed. Quantitative data were obtained on plant coverage, concealment cover (measured by a coverboard), arthropod diversity and soil seed and fungal sclerotia numbers.

The plant communities were more diverse in control than burn sites and more diverse in the Trail Creek than the Divide sites. Tree and shrub coverage and log concealment were greater in the controls than their respective burns. The amount of bare ground was greater in the Divide Burn than any other site. No differences in forb and graminoid coverage and vegetative concealment were found between either burn and control sites. No differences between the burns and controls were found in numbers of either plant seeds or fungal sclerotia (*Cenococcum geophilum*) recovered from the top 5 cm of the soil samples. Total arthropod numbers in the burn sites were similar to their respective control sites, but the burns supported larger numbers of dipterans and fewer araneidans and acarinans than the controls.

Ten species of small mammals were collected in the study areas. *Clethrionomys gapperi* was the most abundant small mammal in all four sites, and fungi were the most important items in their diets ($\bar{X}$ range 77-98% relative density in all four sites). *Peromyscus maniculatus* were more numerous in the burn sites than in the control sites, and arthropods were the most important item in all sites ($\bar{X}$ range 52-92%). *Eutamias amoenus* were more numerous in the burns than in the controls and exhibited a large amount of individual variation in food habits. Arthropods, seeds, fungi, and forbs were all important in their diets. The hypothesis that numbers of *Peromyscus maniculatus* in the burns were limited by competition with *Clethrionomys gapperi* was tested by removal of *Clethrionomys gapperi* from two 0.36 ha plots in the Divide Burn; numbers of *Peromyscus maniculatis* were not affected.

INTRODUCTION

Fires have always been an integral part of the natural environment (Despain 1972; Houston 1973). In recognition of the ecological significance of forest fires and in an attempt to fulfill their goal of maintaining an area in as natural condition as possible, Yellowstone National Park in 1972 established a fire policy whereby natural fires were allowed to burn within designated areas. This natural fire zone includes 697,000 hectares.

The small mammal community is an important component of the ecosystem as a food source for predators, as consumers of seeds, arthropods and vegetation, and as a dispersal mechanism for fungal spores. The reaction of these animals to changes in the environment is important to our understanding the processes that occur in the ecosystem. Bendell (1974) summarized much of the literature concerning the effects of fire on small mammals and found that few studies have investigated the changes in species composition and abundance of small mammals after recent natural fires. Gashwiler (1970) and Tevis (1956) studied the relationship between small mammals and fire after timber management practices. Taylor (1973) and Fox (1978) discussed changes following wildfires over long periods of time. The Park Service's current fire policy offers a unique opportunity to study the small mammal responses during the first few years postburn. The purpose of this study was to describe some of the effects that two recent natural fires have had upon the small mammal communties and their food habits.

Specific objectives of the study were to record any changes in abundance or composition of species of small mammals in the burn areas as compared to the non-burn or control areas. The food habits of *Clethrionomys gapperi* (red-backed vole), *Peromyscus maniculatus* (deer mouse), and *Eutamias amoenus* (yellow pine chipmunk) were examined, and the distribution and abundance of vegetation, seeds, and arthropods which serve as food sources for the small mammals were sampled. The possibility of competition between *Peromyscus* and *Clethrionomys* under natural conditions was experimentally tested in one of the burns in an attempt to explain the low numbers of *Peromyscus* caught.

Two recently (2 and 4 years postfire) burned sites in Yellowstone National Park were chosen for the research: the Divide Burn located near the South Arm of Yellowstone Lake, and the Trail Creek Burn located north of Trail Lake. Field work was conducted from June to September of 1978 and 1979.

This project was supported during the first year by a grant from the National Park Service. The University of Wyoming-National Park Service Research Center supported the second year's research.

METHODS

Two areas that had burned recently were selected. The first, the Divide Burn (DB), is located near the west shore of the South Arm of Yellowstone Lake (5528 - 49058 UTM) and was started by lightning in July 1976 (Figure 1). Approximately 656 ha of spruce-fir forest were affected by the fire. The actual study site in the burn was selected on the basis of homogeneity of degree of burn and revegetation. The site was located in an area of relatively level terrain at an elevation of 2310 meters. Edges (lakeshore, forest, streams) were avoided. A nearby control site was selected to represent the vegetation existing in the study site before the fire. The Divide Control (DC) is located to the north of the burn area in a mature spruce-fir forest with similar slope and elevation to that in the burn.

The second study area, the Trail Creek Burn (TCB), is located approximately 2 miles south of the Southeast Arm of Yellowstone Lake (5660 - 49036 UTM) at an elevation of 2340 meters (Figure 2). The fire started in September 1974 and burned nearly 238 ha of old-growth lodgepole pine forest with spruce-fir regeneration. The burn study site was again selected on the basis of homogeneity of degrees of burn and revegetation. The Trail Creek Control (TCC) is located in a nearby stand of mature lodgepole pine and spruce-fir which is believed to represent conditions of similar vegetation and slope to that existing in the burn before the fire.

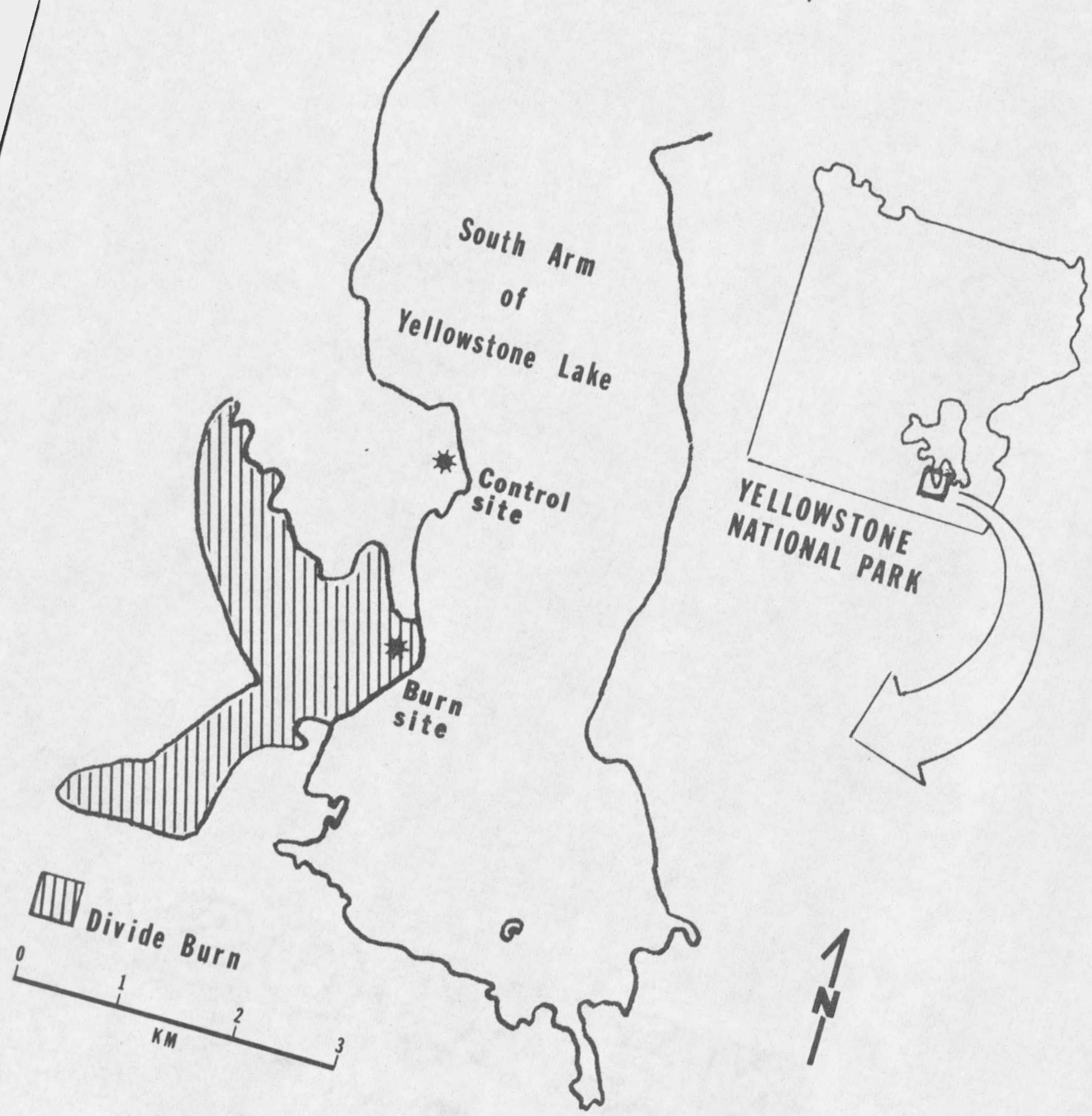

Figure 1. The Divide study area.

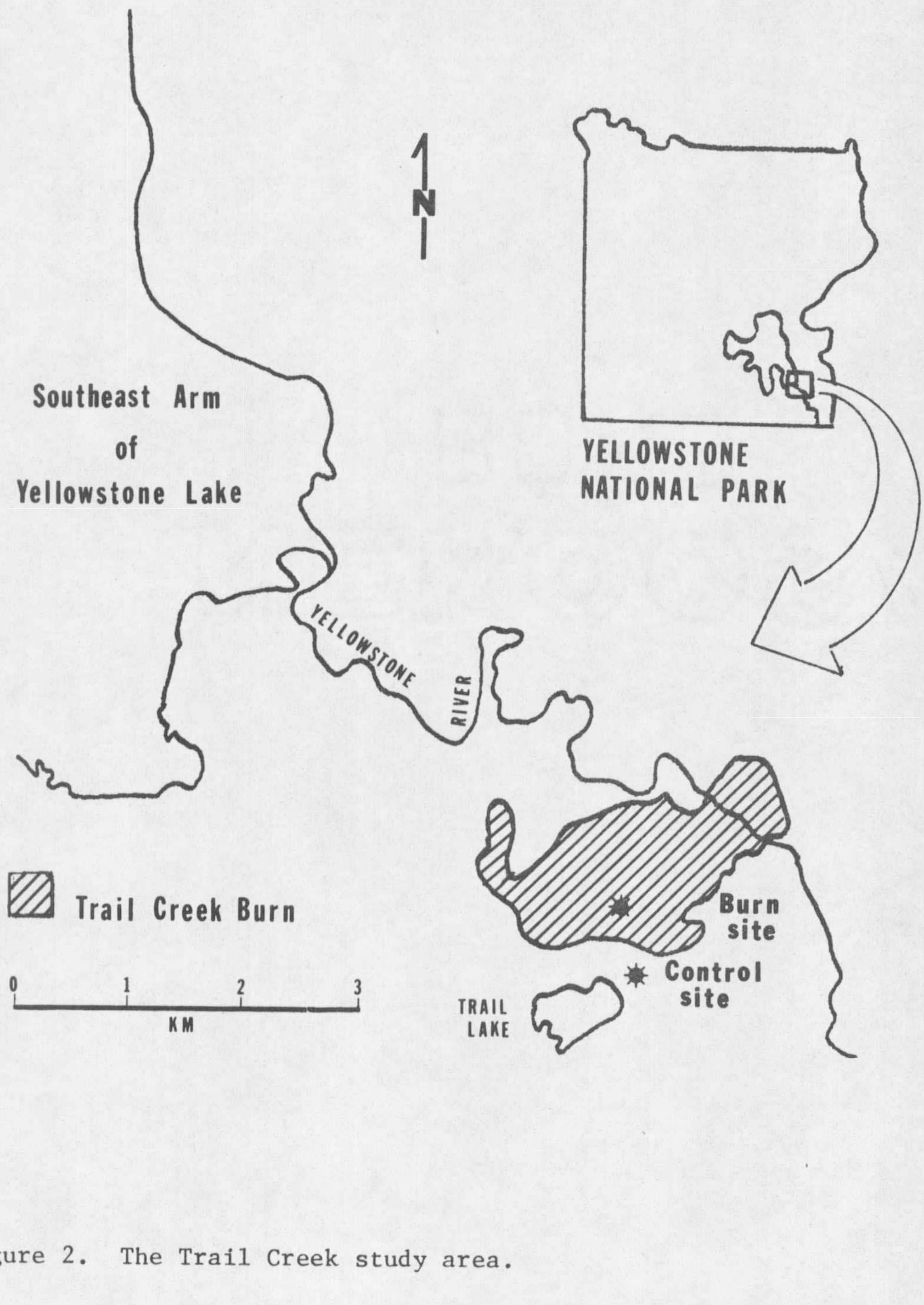

Figure 2. The Trail Creek study area.

Animal Sampling

Small mammals were sampled in each burn and control site by snap-trapping by methods described by Calhoun (1948). An edge site in the Trail Creek area was also sampled. In each area two parallel trap lines were established, each line with 20 trap stations spaced 15 meters apart. Three Museum Special traps were placed at each trap station and were baited with a mixture of peanut butter and oatmeal. Traps were set for three consecutive nights during each trap period. Traps were left operational during the day to be available to diurnal animals. There were two trapping periods (early summer and late summer) for each site during each year. The early summer trap periods in all four sites occurred from mid-June through the first week of July during both years. The late summer trap periods occurred from mid-August through the first week of September for both years. Captured animals were identified by species. Sex and reproductive condition were noted. Adults and subadults were identified on the basis of size. Stomachs were removed from *Clethrionomys gapperi*, *Peromyscus maniculatus*, and *Eutamias amoenus* and preserved in salt.

Shrew populations were sampled using pitfall traps once in July during the first year in Divide Burn and Divide Control. One three pound coffee can was placed in the ground near each trap station; 40 traps were used in each site. The pitfall traps were checked for three consecutive days.

Relative indices of pocket gophers in both burn and control sites were determined by mound counts (Reid et al. 1966) during August of the second year. A 285 m belt transect was centered along each snap-trap line. Mounds within 5 m on either side of the line were leveled, and 48 hours later new mounds and plugs were recorded.

Interspecific competition was experimentally tested between *Peromyscus maniculatus* and *Clethrionomys gapperi* in 1979. Three live trap grids were established in the Divide Burn outside the snap-trap lines. Each grid was 0.36 ha and consisted of 49 Sherman live traps baited with peanut butter and oatmeal. Traps were spaced 10 m apart with seven traps to a side. Traps were kept open 24 hours and checked in the morning. The three grids were trapped simultaneously from July 14-22. For the first four nights all captured *Peromyscus* and *Clethrionomys* were toe-clipped for identification and released. For the next five nights *Clethrionomys* were removed from grids #2 and #3. Grid #1 served as a control; no *Clethrionomys* were removed. One month later, all three grids were retrapped for four successive nights to obtain numbers of *Clethrionomys* and *Peromyscus*.

Arthropods were collected in the four sites during 1978 by using pitfall traps (Morrill 1975). Two pitfall traps were placed on either side of the snap-trap stations along both trap lines in each area. Arthropods were collected for three days during each snap-trapping period and stored in 70% alcohol until they were later identified in the laboratory.

The stomachs collected during the snap-trapping periods were oven dried at $50^{o}C$ and sent to the Colorado State University Composition Analysis Laboratory for dietary analysis. Their methods follow those described by Sparks and Malechek (1968) for microscopic technique. Identification and percentages of orders of arthropods found in the stomachs were determined by examining 40 low power fields per specimen with a compound scope. Identification of vegetation and percentages of arthropods and vegetation types were determined by examining 40 high power microscope fields per specimen.

Vegetation Measurement

During 1978, a list of plant species and their frequencies was made by recording species found within 3.14 m^2 circular plots (Raunkiaer 1934) located at each trap station along the two trap lines established in each site. Identification of plant species and nomenclature follow Hitchcock and Cronquist (1973).

Coverage of trees, shrubs, forbs, graminoids, bare ground, and logs was determined in 1978 by recording per cent cover of these categories following a modified cover class scale (Bailey and Poulton 1968) based on Daubenmire's (1959) work. Coverages were determined from the same 40 circular plots used to record species of plants in each site.

Populations of seeds present in the soil during the late summer trapping period of 1978 were estimated from soil samples taken along the established trap lines. Two soil cores were collected with an Oakfield Apparatus at each trap station; thus 80 samples were taken from each site. Each core sample was divided into three soil depths: 0-2 cm, 2-5 cm, 5-10 cm. Soil samples from each depth were pooled and stored in bags until they were examined in the lab. Seeds were separated from the soil in the laboratory following the methods of Barbour and Lange (1967) and Reichman (personal communication). At the same time fungal sclerotia were extracted from the soil and counted. The fungi were sent to J. Trappe (USFS, Corvallis, Oregon) who identified them as sclerotia of the ectomycorrhiza forming fungus *Cenococcum geophilum*. The viable sclerotia vary from .05 to 4 mm or more in diameter and are jet black, hard, smooth and mostly spherical (Trappe 1969). This fungus occurs in temperate to alpine climatic zones in North America and is known to associate with several species of conifers (Trappe, 1964).

Vertical concealment cover was estimated by use of a coverboard (Jones 1968). The board measured 25 cm by 50 cm and was divided into 50 squares. Each square (measuring 5 cm by 5 cm) represented the approximate size of a small mammal that could be concealed by vegetation or log cover. The board was placed vertically at each trap station and viewed from a distance of 5 meters. Numbers of squares covered by vegetation or logs were recorded.

Statistical analyses were made according to Snedecor and Cochran (1967). Means were compared using the MSU Statistical Library T-Grouped and Compare Test (MSUSTAT program developed by R. E. Lund, Dept. of Mathematics) available at the Montana State University Computer Center.

RESULTS

Vegetation Measurement

Species composition for each study site is presented in Table 1. There were some differences in numbers and kinds of plants between the burn and control sites and between the two areas. No statistical comparisons were made from the descriptive data.

Similar tree species were found in both control sites. No live trees occurred in the burn sites. Shrubs were generally more frequent in the Trail Creek area than the Divide area. One shrub, *Vaccinium scoparium*, was common in all four sites. More graminoid species were found in the Trail Creek area than the Divide area. *Carex geyeri* was common in all sites although it was more abundant in the two burn sites than in the control sites. Forbs were also generally more abundant in the Trail Creek area. The largest number of species was found in the TCC. Few forbs were found in the DB. *Arnica cordifolia* was common to all four sites and was found frequently. *Aster foliaceus*, *Epilobium angustifolium*, and *Lupinus argenteus* were also common to all four sites but occurred less frequently in the Divide area than in the Trail Creek area.

Mean canopy coverages for trees, shrubs, forbs, graminoids, logs, and bare ground in each study site are reported in Table 2. Significant differences between means, as measured by t-tests, occurred between burn and control sites and between the areas. Both control sites exhibited

Table 1. Frequency (1=10%) of plant species found in the 3.14 m^2 circular plots. Forty plots, located along the snap-trap lines, were examined in each burn and control site in 1978. The forty plots were divided into four sequential groups of 10 and labeled: a, b, c, d. Within each category (trees, shrubs, graminoids, and forbs) plant species that are apparently tolerant of fire are listed first; those appearing intolerant are listed last.

	DIVIDE								TRAIL CREEK							
SPECIES	BURN				CONTROL				BURN				CONTROL			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
TREES																
Pinus contorta					8	5	9	3			1		3	8	9	9
Abies lasiocarpa					4	9	8	*					7	7	9	7
Picea engelmannii					8	3	5	7					5	5	1	3
Pinus albicaulis						3	6	5					5	5	1	3
SHRUBS																
Vaccinium scoparium	3	7	5	7	*	9	6	5	7	5	7	5	9	5	7	6
Linnaea borealis									3	1	1		5	5	4	7
Rosa acicularis									2		1					
Sherpherdia canadensis		1					1									
Vaccinium globulare		1														
Lonicera utahensis	1			1	1								3	4	5	5
Juniperus communis					2									1	1	
Sambucus racemosa					1			2								
Chimaphila umbellata							1								1	
GRAMINOIDS																
Carex geyeri	*	9	*	9	2	3	6	3	6	3	4	5		2	2	1
Calamagrostis canadensis			4	1	3	3		3	6	9	5	4	3			2
Carex xerantica									2	2		1				
Trisetum spicatum												1				
Bromus anomalus												1	8	6	1	6
Poa nervosa												2	1	2	3	2
Stipa occidentalis																1
Agropyron caninum																1

Table 1. Continued.

SPECIES	DIVIDE								TRAIL CREEK							
	BURN				CONTROL				BURN				CONTROL			
	a	b	c	d	a	b	c	d	a	b	c	d	a	b	c	d
FORBS																
Arnica cordifolia	7	*	7	7	8	7	4	6	9	3	8	8	7	2	1	3
Aster foliaceus	5	3	6	6	1	2			5	6	3	4	4	7	9	7
Epilobium angustifolium	2	6	4	8	2	3		1	9	9	8	8	8	9	*	*
Lupinus argenteus	2	1			3	1		1	9	6	5	6	3	8	8	7
Equisetum arvense									6	7	1	4	2		1	1
Galium boreale									3	1	1	1		4	1	3
Thalictrum occidentale										2	1	1	2			1
Agoseris glauca									2	2			2	1		
Astragalus miser									1	3						4
Viola sp.				1	1						1	1		1	1	3
Solidago multiradiata			1										1	2		3
Fragaria virginiana					3	4	2	2		1	1	1	5	7	9	8
Antennaria racemosa					7	2										
Osmorhiza depauperata					2	1							4		3	4
Aquilegia flavescens					3	2							2			
Pyrola secunda	1								2				3	1	2	2
Campanula rotundifolia														2	3	1
Achillea millefolium														2	2	2
Smilacina stellata															2	2
Phlox multiflora																4
Gentiana amarella															1	3
Taraxacum officinale													1			
Potentilla gracilis																1
Hieracium albiflorum				1												
Antennaria parvifolia			1													

* Equals 10.

Table 2. Mean canopy coverage in per cent for each category within 40 3.14 m^2 circular plots in each of the four study sites. Standard deviations are in parentheses.

	DB		DC	TCB		TCC
TREES	0.0	*	28.0	0.6	*	28.0
	(0.0)		(17.8)	(4.0)		(15.5)
SHRUBS	2.4	*	26.4	3.6	*	30.0
	(2.4)		(24.7)	(4.5)		(20.4)
			*			
FORBS	7.5		10.5	36.2		31.0
	(8.8)		(11.0)	(13.6)		(12.3)
				*		
			*			
GRAMINOIDS	5.9		3.6	19.4		12.7
	(8.2)		(6.7)	(20.4)		(12.7)
				*		
LOGS	29.5	+	38.6	26.2		29.8
	(18.1)		(18.0)	(16.8)		(20.8)
				*		
			*			
BARE GROUND	57.8	*	26.8	11.3		9.2
	(22.0)		(23.3)	(9.7)		(12.3)
				*		

* Indicates significance at $p \leq .01$, *t*-test.

\+ Indicates significance at $p \leq .05$, *t*-test.

greater tree coverage than either burn site ($p \leq .01$). Shrubs were more dominant in the controls than in the burn sites ($p \leq .01$). There were no differences in forb and graminoid coverage between the burn and control site in either area. However, forb and graminoid coverage was greater in the TCC than in the DC and greater in the TCB than in the DB ($p \leq .01$). Coverage of logs was greater in the DC than in any other site ($p \leq .05$). The amount of bare ground coverage was significantly ($p \leq .01$) greater in the Divide burn and control sites than in the corresponding Trail Creek sites. Significantly ($p \leq .01$) more bare ground occurred in the Divide Burn than in the DC.

Coverboard data was recorded in Table 3. No differences were found in the amount of vegetative concealment between the burn and control sites of either the Divide or Trail Creek area. However, significantly ($p \leq .01$) greater amounts of vegetation for possible concealment were found in the Trail Creek sites as compared to the Divide sites. There were differences found in concealment by logs between the burn and control sites. Both control sites exhibited greater amounts of logs than their respective burn sites ($p \leq .05$).

Results of soil sampling are reported in Tables 4 and 5. Species of seeds separated from the soil are not given due to difficulties in their identification. The numbers of seeds were converted to numbers of seeds per 100 g of soil. Means were computed from the three replicates of each layer and were compared by *t*-tests. When all layers and

Table 3. Per cent mean cover of vegetation and logs for possible concealment of small mammals in the four study sites. Estimates were made using a coverboard. Standard deviations are in parentheses.

	DB	DC	TCB	TCC
VEGETATION	6.5 (12.4)	6.8 (8.6)	18.4 (22.8)	25.3 (26.5)
LOGS	12.7 (21.3)	31.5 (38.5)	5.6 (14.8)	18.3 (29.3)

+ indicates significance at p $\leq$ .05, *t*-test.

* indicates significance at p $\leq$ .01, *t*- test.

replicates were combined there was no difference between numbers of seeds in the DC as compared to DB (Table 4). However, there were differences observed between layers within each site. In both sites (burn and control) the top layer (0-2 cm) had significantly (p $\leq$ .05) more seeds than the bottom (5-10 cm) layer.

Total seed numbers were significantly (p $\leq$ .05) greater in the TCC than in the TCB. Differences between layers within each site were also noted. In the control site only the first two layers were different (p $\leq$ .05). In the burn site the first layer had significantly (p $\leq$ .05) more seeds than either the top or the middle layers.

Since the top 5 cm may be important to digging rodents, the 0-2 cm layer and the 2-5 cm layer of each site were combined and compared.

Table 4. Calculated number of seeds found in the three depth layers sampled in the four study sites. Mean numbers of seeds/m^2 soil were calculated from $\overline{X}$ seeds/100 g soil and kg soil/m^2.

AREA	LAYER cm	No. of seeds/100 g soil[1] REPLICATE 1	2	3	$\overline{X}$ seeds per 100 g soil (s)	kg soil/m^2	$\overline{X}$ seeds/m^2
DB	0–2	44	15	10	23.0 (18.4)	3.0	690
	2–5	12	0	0	4.0 (6.9)	3.0	120
	5–10	0	0	0	0.0 (0.0)	3.1	0
DC	0–2	34	9	40	28.0 (16.4)	4.7	1316
	2–5	20	11	8	13.0 (6.2)	3.5	455
	5–10	0	0	11	4.0 (6.4)	2.8	112

Table 4. Continued.

AREA	LAYER cm	No. of seeds/100 g soil[1] REPLICATE 1	2	3	$\overline{X}$ seeds per 100 g soil (s)	kg soil/ m^2	seeds/ m^2
TCB	0-2	46	68	26	46.7 (21.0)	2.7	1261
	2-5	11	0	12	7.7 (6.7)	2.4	185
	5-10	0	11	0	3.7 (6.4)	2.4	89
TCC	0-2	72	88	109	88.7 (18.6)	3.8	3371
	2-5	17	19	77	37.7 (34.1)	3.2	1206
	5-10	89	45	0	44.7 (44.5)	2.4	1073

+ Indicates significance at $p \leq .05$, *t*-test.

[1] All soil weights are actually weights of organic matter separated from the soil.

Table 5. Calculated number of sclerotia of *Cenococcum geophilum* found in the three depth layers sampled in the four study sites. Mean numbers of sclerotia/m^2 soil were calculated from $\overline{X}$ sclerotia/100 g soil and kg soil/m^2.

AREA	LAYER cm	No. of sclerotia/100 g soil[1] REPLICATE 1	2	3	$\overline{X}$ sclerotia per 100 g (s)	kg soil/m^2	$\overline{X}$ sclerotia/m^2
DB	0-2	178	344	231	251 (84.8)	3.0	7530
	2-5 +	318	447	516	427 (100.5)	3.0	12810
	5-10	678	456	714	422 (212.1)	3.1	13082
DC	0-2	175	103	48	109 (63.7)	4.7	5123
	2-5	758	267	227	417 (295.7)	3.5	14595
	5-10	481	105	989	525 (443.6)	2.8	14700

Table 5. Continued.

AREA	LAYER cm	No. of sclerotia/100 g soil[1] REPLICATE 1	2	3	$\bar{X}$ sclerotia per 100 g (s)	kg soil/ m^2	$\bar{X}$ sclerotia/ m^2
TCB	0-2	310	369	325	335 (30.7)	2.7	9045
	* 2-5 *	932	1021	625	859 (207.8)	2.4	20616
	5-10	957	591	807	785 (184.0)	2.4	18840
TCC	0-2	36	97	78	70 (31.2)	3.8	2660
	* 2-5 +	940	454	368	587 (308.4)	3.2	18784
	5-10	1044	1011	733	929 (170.8)	2.4	22296

+ Indicates significance at $p \leq .05$, *t*-test.

* Indicates significance at $p \leq .01$, *t*-test.

[1] All soil weights are actually weights of organic matter separated from the soil.

No statistically significant differences were found between the control and burn sites of either the Divide or Trail Creek areas. No significant differences were found when comparing both burn sites; however, the TCC had significantly ($p \leq .05$) more seeds than the DC.

Means of numbers of sclerotia of *Cenococcum geophilum* per 100 g of soil were compared by *t*-tests (Table 5). No differences in total numbers from all replicates were found between burn and control sites in either area. However, differences were found within sites. The top layer in the DB had significantly ($p \leq .05$) fewer sclerotia than the middle layer. No significant differences occurred in the DC site. The top layers had significantly fewer sclerotia than the middle layers in the TCB ($p \leq .01$) and the TCC ($p \leq .05$). Similarly, the top layers had significantly fewer sclerotia than the bottom layers in the TCB and the TCC ($p \leq .01$). No significant differences were found between numbers of sclerotia in the top 5 cm of soil between the two burn sites or the two control sites.

Animals

Snap-trapping

Data from the early and late summer trap periods were combined in order to increase the sample sizes for statistical comparisons. Although there were differences between the two trap periods, the differences were similar at each site. These differences exhibited three general trends observed during the late trap period: increased pregnancy rates, decreased litter size, and increased numbers of subadults captured. Numbers of individuals were compared by the chi-square test.

Data from the two years were kept separate as significant differences occurred in numbers of animals caught (Tables 6 and 7). In all four sites numbers of *Clethrionomys* were significantly ($p \leq .01$) greater during the second year. Numbers of *Peromyscus* increased significantly ($p \leq .05$) in the TCB and the TCC during the second year. No other species showed a significant increase during the second year.

Several differences were noted between the two areas. During the first year the DB had significantly ($p \leq .01$) more *Peromyscus* than the TCB. In the second year *Clethrionomys* numbers were significantly ($p \leq .01$) greater in both Divide sites as compared to the corresponding Trail Creek sites.

In the Divide area, species and numbers of individuals varied between the burn and control sites and between the two years. The most abundant small mammal was *Clethrionomys* in both the burn and control site during 1978 and 1979. Significantly more red-backed voles were caught in the control than in the burn during 1978 ($p \leq .05$) and 1979 ($p \leq .01$). *Peromyscus* and *Eutamias* were captured in greater numbers in the burn site than in the control site for both years ($p \leq .05$). Two species of shrews (*Sorex*) were captured in both the burn and control

Table 6. Total numbers of small mammals snap-trapped during 1978 in the four study sites and an edge site. Numbers in parentheses are total trapnights (total number of traps minus the number of empty snapped traps).

SPECIES	STUDY SITE				
	DB (510)	DC (580)	TCB (653)	TCC (604)	EDGE (337)
Clethrionomys gapperi	16	36	12	48	31
Peromyscus maniculatus	14	5	2	0	0
Eutamias amoenus	10	2	13	8	7
Sorex cinereus	3*	4	2	5	0
Sorex vagrans	2	2	0	0	0
Sorex sp.	0	3	0	0	0
Microtus montanus	0	0	1	1	0
Glaucomys sabrinus	0	2	0	0	0
Tamiasciurus hudsonicus	0	0	0	0	1

* Captured in insect pitfall traps but included in the count.

Table 7. Total numbers of small mammals snap-trapped during 1979 in the four study sites. Numbers in parentheses are total trapnights (total number of traps minus the number of empty snapped traps).

SPECIES	STUDY SITE			
	DB (651)	DC (571)	TCB (654)	TCC (627)
Clethrionomys gapperi	66	131	29	110
Peromyscus maniculatus	17	1	10	7
Eutamias amoenus	13	4	13	8
Sorex cinereus	2	4	0	1
Microtus montanus	0	0	3	1
Microtus pennsylvanicus	0	0	1	0
Microtus sp.	0	0	0	1
Zapus princeps	2	0	0	0
Tamiasciurus hudsonicus	0	0	0	1

sites during both years, although only *Sorex cinereus* was represented the second year. Two flying squirrels, *Glaucomys sabrinus*, were caught in the DC the first year. Two *Zapus princeps* were caught in the DB in 1979.

Species and numbers of individuals in the Trail Creek area also varied between the burn and the control sites and between the two years. The most abundant small mammal in the control and edge sites for both years was *Clethrionomys*. These were also the most abundant small mammal in the burn site in 1979 but not in 1978. Significantly ($p \leq .01$) greater numbers of red-backed voles occurred in the control than in the burn during both years. Significantly ($p \leq .01$) greater numbers were also captured in the edge than in the burn site in 1978. *Eutamias* was the next most abundant small mammal in the Trail Creek sites. *Peromyscus* was captured only in the burn site during 1978. By the second year deer mice were captured in both the burn and control sites. *Sorex cinereus* was the only shrew species captured and was present in both sites.

Some differences in age groups, sex ratios, and occurrence of pregnancy were noted between the areas and the two years. Adult males comprised the largest component of the *Clethrionomys* population in all sites and during both years. Pregnancies occurred in all sites. During the first year more male *Peromyscus* were captured than females in all sites. Pregnancies occurred only in the two burn sites. By the second year female *Peromyscus* outnumbered males. Again no pregnancies were recorded in the control sites. In the first year female *Eutamias* outnumbered the males in all sites except the DB. During the second year male *Eutamias* outnumbered the females in all sites except the TCB. No pregnancies were noted in any of the females.

Live trapping

Interspecific competition was tested by removing *Clethrionomys* and determining whether *Peromyscus* numbers increased. Results of live trapping on the three grids located outside the snap-trap line in the DB site are listed in Table 8. Numbers of *Peromyscus* and *Clethrionomys* were tested with chi-square. No differences were found between numbers caught during the baseline trapping and the retrap period in any of the plots. Numbers of *Peromyscus* and *Clethrionomys* in each plot were tested for differences between plots; no differences occurred. Results of the competition experiment are also examined by comparing relative increases or decreases in numbers of *Peromyscus* (Table 9). In all plots the ratio of numbers of *Peromyscus* to numbers of *Clethrionomys* decreased. Removal of *Clethrionomys* did not result in relative increases in numbers of *Peromyscus*.

Pocket gophers

Evidence of pocket gophers (*Thomomys talpoides*) in the two study areas, Divide and Trail Creek, was surveyed during 1979. No gopher

Table 8. Numbers of *Clethrionomys* and *Peromyscus* caught during live trapping competition study in the DB site. Plot 1 was the control grid. Plots 2 and 3 were the experimental grids (*Clethrionomys* removed).

GRID	TRAP PERIOD Baseline	Retrap
Plot 1 (Control)	9 *Clethrionomys*	17 *Clethrionomys*
	5 *Peromyscus*	5 *Peromyscus*
Plot 2	11 *Clethrionomys*	10 *Clethrionomys*
	7 *Peromyscus*	4 *Peromyscus*
Plot 3	5 *Clethrionomys*	11 *Clethrionomys*
	8 *Peromyscus*	12 *Peromyscus*

Table 9. Ratios of *Peromyscus* live-trapped for each *Clethrionomys* caught during the experimental competition study.

GRID	TRAP PERIOD Baseline	Retrap	EFFECT
Plot 1 (Control	.55	.29	decrease
Plot 2	.64	.40	decrease
Plot 3	1.60	1.10	decrease

mounds were found along the belt transect in either the Divide burn or control site. However, one young male was captured in a shrew pitfall trap in the burn site. Also several mounds were noted within the burn area but outside the study site. These mounds were found on sloping terrain near the lakeshore and on a slope near a creek bottom.

Pocket gopher activity was found within the study sites on the Trail Creek area. Ten mounds were found along the belt transect in the burn site. Two mounds were found in the control site.

Food Habits

Stomach samples from *Clethrionomys*, *Peromyscus*, and *Eutamias* were analyzed to compare food habits in the four study sites during two years. Results are reported in per cent relative density of food items found in the stomachs. Relative density is a reliable estimate of per cent composition by dry weight (Sparks and Malechek, 1968). Data from both trapping periods in 1978 (early and late summer) were combined to increase sample size for statistical comparisons with the *t*-test. Only one trap period (early) was sampled in 1979. One significant ($p \leq .01$) difference between early and late summer in 1978 occurred: stomachs of *Eutamias* captured in the DB contained more vegetative matter during the early period and more arthropods during the late period.

All stomachs sampled from *Clethrionomys* were collected during 1978. In the Divide area, fungi were the most frequent food items and had the highest relative density in their diet (Table 10). However, they ate significantly ($p \leq .01$) fewer fungi in the burn (77%) than in the control (98%) site. Forbs were eaten more frequently in the burn and in significantly ($P \leq .01$) greater amounts (22%) than in the control (5%) site. *Astragalus* comprised 90% of the forbs in stomachs of red-backed voles from the DB. Only minor amounts of the other food types were found in the stomachs although arthropods occurred frequently in the diets. Four orders of arthropods were found in the diets of red-backed voles from the DB; two orders were found in those from the DC (Table 11).

Diets of *Clethrionomys* caught in the Trail Creek area were similar to those from the Divide area. Fungi were again the primary foods in both the burn and control sites, and made up a significantly ($p \leq .01$) greater percentage of the diet in the TCC (95%) than in the TCB (80%). Forbs comprised a larger part of the diet in the burn than in the control ($p \leq .01$). *Lupinus* was the most frequently (95%) eaten genus. Other foods were found in *Clethrionomys* stomachs in only minor amounts.

The food habits of *Peromyscus* varied between sites and between years (Table 12). In the Divide area during 1978, arthropods comprised the largest percentage of the diets. Significantly ($p \leq .05$) more arthropods were eaten in the burn (86%) than in the control site (52%). Dipterans and hymenopterans were common arthropods in the stomachs of deer mice from the control site (Table 13). Hymenopterans, lepidopterans

Table 10. Stomach contents of *Clethrionomys gapperi* caught in the four study sites. Samples are from 1978. Mean percentages ($\bar{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 high power microscope fields per specimen.

FOOD TYPE		SITE					
		DB (n=16)		DC (n=34)	TCB (n=12)		TCC (n=42)
Arthropods	$\bar{X}$	.89		1.00	5.44		.96
	s	1.08		2.65	15.38		1.42
	f	.56		.35	.50		.55
Grass		.43		.02	0.00		.03
		1.57		.10			.18
		.13		.03			.02
Forbs		21.84	— * —	.05	8.95	— * —	2.22
		37.38		.17	12.06		5.26
		.69		.08	.75		.43
Fungi		76.76	— * —	98.30	80.06	— * —	95.34
		36.75		3.20	29.66		6.87
		.94		1.00	1.00		1.00
Seed		0.00		.61	5.46		.53
				1.38	18.90		1.40
				.21	.08		.26
Other		.08		.02	.09		1.70
		.33		.10	.21		2.08
		.06		.03	.17		.36

* Indicates significance at $p \leq .01$, *t*-test.

Table 11. Orders of arthropods found in stomachs of *Clethrionomys gapperi* from the four study sites sampled in 1978. Mean percentages ($\bar{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 low power microscope fields per specimen.

ORDER		SITE			
		DB (n=16)	DC (n=34)	TCB (n=12)	TCC (n=42)
Coleoptera	$\bar{X}$	.10	.05	.04	.13
adult	s	.43	.31	.15	.43
	f	.06	.03	.08	.10
Diptera		.27			.02
		1.10	0.00	0.00	.15
		.06			.02
Hymenoptera		.21	.20	.10	.79
		.75	.60	.33	2.80
		.06	.17	.08	.21
Lepidoptera		.30	0.00	2.58	.91
		.89		4.70	2.32
		.19		.25	.24
Unknown		0.00	0.00	.10	.08
				.34	.31
				.08	.10

Table 12. Stomach contents of *Peromyscus maniculatus* caught in three study sites during two years. Mean percentages ($\bar{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 high power microscope fields per specimen.

FOOD TYPE		SITE 1978 DB (n=12)		1978 DC (n=5)	1978 TCB (n=3)	1979 DB (n=10)	1979 TCB (n=5)
Arthropods	$\bar{X}$	85.53	- + -	51.74	92.07	88.52	52.85
	s	22.37		20.63	1.96	24.78	36.30
	f	1.00		1.00	1.00	1.00	1.00
Grass		.28		.41	0.00	0.00	1.10
		.66		.91			2.50
		.17		.20			.20
Forbs		7.39		7.80	6.53	11.06	18.41
		13.78		16.64	.09	24.53	12.37
		.67		.40	1.00	.70	1.00
Fungi		0.00		1.41	0.00	0.00	6.26
				.39			8.74
				.60			.40
Seed		6.80	- + -	38.66	.70	.24	21.25
		19.96		25.40	1.21	.43	25.97
		.33		1.00	.33	.30	1.00
Other		0.00		0.00	.70	.12	.13
					.61	.37	.29
					.67	.10	.20

+ Indicates significance at $p \leq .05$, *t*-test.

Table 13. Orders of arthropods found in stomachs of *Peromyscus maniculatus* from three study sites sampled during two years. Mean percentages ($\overline{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 low power microscope fields per specimen.

ORDER		1978 DB (n=12)	1978 DC (n=5)	1978 TCB (n=3)	1979 DB (n=10)	1979 TCB (n=5)
Araneida	$\overline{X}$	0.00	0.00	0.00	2.53	2.55
	s				2.25	1.44
	f				.90	1.00
Coleoptera adult		1.34	.95	.94	6.33	3.11
		3.14	1.59	1.63	10.90	5.87
		.25	.60	.33	1.00	.80
Coleoptera larvae		7.10	.25	0.00	.78	0.00
		24.60	.55		1.51	
		.08	.20		.40	
Diptera		1.25	7.00	0.00	21.56	.82
		3.59	7.19		30.38	1.25
		.25	.80		.60	.60
Hemiptera		0.00	2.54	0.00	0.00	0.00
			2.11			
			.80			
Homoptera		.77	0.00	1.68	0.00	.45
		2.66		2.90		1.01
		.08		.33		.20
Hymenoptera		12.82	7.18	34.11	29.19	16.50
		18.74	3.27	56.04	37.00	24.58
		.75	1.00	1.00	.90	1.00
Lepidoptera		11.35	1.65	28.62	14.43	8.16
		23.45	3.46	25.21	24.08	10.25
		.50	.40	.67	.90	1.00

Table 13. Continued.

ORDER	SITE 1978 DB (n=12)	1978 DC (n=5)	1978 TCB (n=3)	1979 DB (n=10)	1979 TCB (n=5)
Neuroptera	.03 .10 .08	0.00	0.00	0.00	0.00
Unknown	4.70 12.20 .40	.39 .63 .40	.09 .16 .37	.45 1.42 .10	0.00

+ Indicates significance at p $\leq$ .05, *t*-test.

and coleopterans comprised the largest percentage in the burn site. Seeds occurred in the diets of deer mice from the control site more frequently and in significantly ($p \leq .05$) greater amounts (39%) than in the burn site (7%). Forbs were frequently found in the stomachs of deer mice from both burn and control site but did not constitute a large percentage of the diet. Only minor amounts of grass and fungi were found in the stomachs. During the second year (1979) arthropods (89%) were still the principal food items for *Peromyscus* in the DB; however, the percentage of dipterans and hymenopterans found in the stomachs had increased.

Comparisons of diets of *Peromyscus* in the Trail Creek area were difficult because of small sample sizes, but the results were similar to those in the Divide burn. No deer mice stomachs were sampled from the TCC during either year. Only three stomachs were analyzed in the TCB in 1978. The principal food item was arthropods (92%). Of the five orders of arthropods eaten, hymenopterans and lepidopterans were consumed in the greatest amounts (34% and 29% respectively). During the second year of the study arthropods were again the most important food (53%) in the TCB. Seeds (21%) and forbs (18%) were also commonly eaten. *Lupinus* comprised 98% of the identified forbs in the stomachs.

The food habits of *Eutamias* captured in the Divide Burn were compared between 1978 and 1979 (Table 14). No samples were available from the DC during 1979, and only two stomachs were examined the first

Table 14. Stomach contents of *Eutamias amoenus* caught in the four study sites. Two years were sampled. Mean percentages ($\bar{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 high power microscope fields per specimen.

FOOD TYPE		1978 DB (n=10)	1978 DC (n=2)	1978 TCB (n=11)	1978 TCC (n=7)	1979 DB (n=10)	1979 TCB (n=7)	1979 TCC (n=3)
Arthropods	$\bar{X}$	76.50	41.11	17.12	18.96	44.42	23.16	16.34
	s	29.54	56.56	24.21	30.19	20.99	30.64	19.23
	f	1.00	1.00	.17	.85	1.00	1.00	1.00
Grass		.35	0.00	.95	1.63	9.80	4.09	0.00
		1.09		1.98	3.65	14.62	4.80	
		.10		.25	.29	.90	.85	
Forbs		20.68	0.00	5.38	4.60	45.44	17.58	3.79
		29.03		9.88	10.96	21.97	12.20	2.70
		.80		.50	.42	1.00	1.00	1.00
Fungi		1.26	46.74	55.71	6.41	0.00	5.71	0.00
		3.47	66.10	36.88	14.04		13.99	
		.20	.50	.75	.42		.28	
Seed		1.21	10.01	19.21	68.39	0.00	49.05	79.87
		2.11	7.30	18.44	32.64		26.00	18.50
		.40	1.00	.92	1.00		1.00	1.00
Other		0.00	2.13	1.43	0.00	.33	.11	0.00
			2.23	4.16		1.06	2.87	
			1.00	.17		.10	.14	

+ Indicates significance at $p \leq .05$, *t*-test.
* Indicates significance at $p \leq .01$, *t*-test.

year. In the DB arthropods comprised the majority (77%) of the diet during the first year; araneidans, lepidopterans, and hymenopterans were the common orders consumed (Table 15). Forbs (21%) were the next most important food item. The primary forb consumed was *Arnica* (90%). In 1979 the amount of arthropods in the DB diets decreased (44%) and the amount of forbs eaten increased (45%). Both differences were statistically significant ($p \leq .05$). *Arnica* was still a major portion of the forb diet (64%).

The food habits of *Eutamias* varied between sites and years in the Trail Creek area. In 1978 seeds were the principal food items in the control (68%) but not in the burn site (19%, $p \leq .01$). Fungi comprised a larger percentage of the diet in the burn (56%) than in the control site (6%, $p \leq .01$). Similar amounts and orders of arthropods were eaten in the burn site and in the control site, although arthropods occurred more frequently in the stomachs of those from the control site. Forbs comprised only a minor portion of the diets in either site.

During the second year (1979), no differences were found in the diets of *Eutamias* from the burn and control sites. This was possibly due to the small sample size in the TCC (n=3). Foods were consumed in the TCC in 1979 in similar proportions as in 1978 with seeds again the principal food item in the TCC (80%). Seeds became more important in the TCB (49%) with significantly ($p \leq .05$) greater amounts of seeds consumed during the second year in the TCB (49%) than during the first

Table 15. Orders of arthropods found in stomachs of *Eutamias amoenus* in the four study sites sampled during two years. Mean percentages ($\overline{X}$), standard deviations (s), and frequencies (f) are based upon examination of 40 low power microscope fields per specimen.

ORDER		SITE 1978 DB (n=10)	DC (n=2)	TCB (n=11)	TCC (n=7)	1979 DB (n=10)	TCB (n=7)	TCC (n=3)
Araneida	$\overline{X}$	11.64	1.23	.06	.27	0.00	.08	.93
	s	29.06	1.24	.14	.72		.22	1.61
	f	.50	.50	.17	.14		.14	.30
Coleoptera adult		3.30	14.70	.58	1.63	.25	.73	12.00
		6.76	20.79	1.02	2.75	.29	1.16	15.89
		.20	.50	.50	.57	.50	.40	1.00
Coleoptera larvae		.14	3.36	0.00	0.00	0.00	.37	0.00
		.37	4.74				.99	
		.20	.50				.14	
Diptera		1.03	0.00	0.00	0.00	.05	0.00	0.00
		2.52				.16		
		.70				.10		
Hymenoptera		12.00	0.00	1.13	.47	2.73	1.85	1.57
		16.13		1.52	.84	2.44	3.45	2.28
		.90		.58	.43	.80	.57	.67
Lepidoptera		25.40	3.59	14.25	1.51	20.41	4.87	4.07
		20.25	1.63	18.20	3.13	9.84	5.46	4.05
		1.00	1.00	.92	.57	1.00	.57	.30

Table 15. Continued

ORDER	SITE 1978 DB (n=10)	DC (n=2)	TCB (n=11)	TCC (n=7)	1979 DB (n=10)	TCB (n=7)	TCC (n=3)
Orthoptera	0.00	.73	0.00	0.00	0.00	0.00	0.00
		1.03					
		.50					
Unknown	.63	0.00	0.00	.06	.09	0.00	.37
	2.00			.16	.19		.64
	.10			.14	.20		.30

year (19%). Arthropods did not constitute a major part of the diets in either the burn (23%) or the control (16%) but were frequently found in the stomachs. Coleopteran adults comprised the largest percentage of the arthropod foods in the TCC. Forbs were frequently ingested in both the burn and control sites but did not constitute a major portion of the diet (18% and 4% respectively); however, significantly ($p \leq .05$) more forbs were consumed during 1979 in the TCB than during 1978 (5%). *Campanula* flowers comprised 90% of the forb diet in 1979.

Arthropod Estimates

Numbers and types of arthropods found in the Divide and Trail Creek areas in 1978 are reported in Table 16. Variations in the ranked orders of the burn sites were compared to variations in the control sites by Spearman's rank correlation coefficient (r_s) where the coefficient ranges from -1 (complete discordance) to +1 (complete concordance). Differences in numbers within each order of arthropods between burn and control sites were compared by chi square.

Variation in ranked orders between the burn and control sites in each area was not significantly correlated (Divide area r_s=.6152; Trail Creek area r_s=.5364, $p > .05$). Therefore, distribution of orders of arthropods was not the same between burn and control sites of either area. However, when comparing both burn sites and both control sites,

Table 16. Numbers of arthropods caught in 80 pitfall traps in each of the four study sites during 1978.

ORDER	DB		DC	TCB		TCC
	AREA					
Araneida	122	— * —	538	104	— * —	409
Acarina	2	— * —	40	7	— * —	50
Phalangida	0	— * —	21	39		33
Coleoptera	83	— * —	41	67		94
Diptera	326	— * —	62	427	— * —	133
Hemiptera	8		1	14		5
Homoptera	7		1	306	— * —	11
Hymenoptera	152		158	143	— * —	258
Lepidoptera	7		16	24		16
Orthoptera	0		0	3		3
Other	1		8	5		34
Total	708		886	1139		1046

* Indicates significance at $p \leq .01$, chi-square test.

relatively high correlations were found (burns r_s=.7500; controls r_s=.9705, $p \leq .01$). Thus there is agreement among the rankings of orders between the control sites and between the burn sites.

Differences in numbers in each order between burn and control site were tested to account for the lack of correlation found in ranked orders. In both areas numbers of araneidans and acarinans were significantly greater in the control sites than in the burn sites (chi square, $p \leq .01$). Numbers of dipterans were significantly larger in the burn sites than in the controls ($p \leq .01$). Other variations in each area were found. More phalangids were found in the DC than in the DB ($p \leq .01$). More coleopterans were found in the DB than in the DC ($p \leq .01$). Greater numbers of homopterans were found in the TCB than in the TCC ($p \leq .01$). More hymenopterans were found in the TCC than in the TCB ($p \leq .01$).

DISCUSSION

The effects of fire upon small mammal communities vary depending upon several factors, including the type of fire (natural or after clearcutting), habitat, and postburn age. Bendell (1974) suggested the greatest effects upon small mammals occur following fires in forested habitats. Most research on fires in forested habitats have been conducted following timber management practices of bulldozing, slashpiling, and scarification following clearcutting. These methods probably remove most of the log and litter cover and may explain major changes found in small mammal communities. In the two natural burn sites of the present study numerous logs were left and provided cover for small mammals, although bare ground was greater than in the corresponding control sites. The shrub layer decreased significantly in the burns, but there were no significant differences in coverage of forbs and graminoids between burn and control sites.

The Food Resource

Although coverages of the herbaceous layer were similar, species composition differed between the burn and control sites. Diversity of forbs and graminoids were lower in the burn sites. Dominant species were *Arnica*, *Aster*, and *Epilobium* among the forbs and *Carex geyeri* and *Calamagrostis canadensis* among the graminoids.

Ahlgren (1974) reviewed the few studies on effects of fire in fungal populations and reported variations between regions and between different ages of burns. In a Douglas-fir area in the Pacific northwest researchers found fewer fungi in the upper 1½ inches of soil six months after a fire. A second study in the same area also reported a reduction in fungi the first year after a fire. However, other investigators (Ahlgren 1974) reported no postfire decrease in fungi from burns in Minnesota and Ahlgren suggested that fewer fungi may be found after a burn because of the alkaline soil conditions produced by ash. As the ash is leached out and the soil becomes more favorable to some fungi, this important food source becomes available to the small mammals.

The only quantitative data obtained in the present study on fungal food resources were on the sclerotia of *Cenococcum geophilum* recovered from the soil samples. There were no differences in numbers of sclerotia between burn and control sites. However, the data should not be extrapolated to include the several taxa of fungi known to be consumed by small mammals (Maser, Trappe, and Nussbaum 1978) which may respond differently to postburn soil conditions (Ahlgren 1974).

Coniferous seed predation by small mammals has been reported in the range of 3% (Martell and Merritt 1979) to 36% (Radvanyi 1970) through radioactive tagging studies. Few studies have investigated the effect fires have on the seed populations found in the soil. However, Krefting and Ahlgren (1974) studied two areas after wildfires in mixed conifer-hardwood forests and found that in one case seeds preferred by mice decreased in availability between the 5th and 10th year while on the other site a continuous supply of seeds was available after the second growing season.

No significant differences were found in the numbers of seeds in soil depths of 0-5 cm between either burn and control sites. The distribution of seeds among replicates was variable and may have masked any real differences between burn and control sites, as was suggested by data from the Trail Creek area. Most of the seeds were located in the top 5 cm of soil and were therefore available to small mammals.

Post-fire studies of arthropods, although few in number, tend to agree that fire affects types of arthropods differently, Ahlgren (1974) has summarized much of the research prior to 1974 and reported increased numbers of grasshoppers (orthopterans), leafhoppers (homopterans) and possibly ants (hymenopterans) while numbers of beetles (coleopterans) and spiders (araneidans) decreased. Generally, authors feel there is an overall increase in arthropod productivity (Gullion 1967; Hurst 1970). Estimates of arthropod abundance in the present study differ from that reported in the literature. In the two burn sites total numbers of arthropods were similar to the adjacent control sites. Dipterans did increase following fires, and homopterans were more numerous in TCB than in the TCC. Increases of hymenopterans and orthopterans following fire were not noted. Dipterans, hymenopterans and araneidans were common in both burn sites. Gniadek (1977) also reported dipterans and hymenopterans to be common in the same burn sites.

Food Habits

Clethrionomys gapperi

Vascular plant material has been found to comprise a majority of the food types in diets of red-backed voles in many studies, and red-backed voles are thought to be dependent on succulent foods to supplement water intake (Getz 1968). Estimates of vascular plant material in their stomach contents range from 59-100% by volume (Schloyer 1977; Clark 1973). Fungi have also been reported to be an important item in the diet of red-backed voles. Williams and Finney (1964) found Endogonaceae (a hypogeous Phycomycete) comprised 5-100% of the volume of *Clethrionomys gapperi* stomachs in northwest Wyoming and northcentral Colorado. Stomachs of *Clethrionomys* collected in a Colorado subalpine forest revealed a very specific diet of fungi; by August 80% of the volume was fungi (Merritt and Merritt 1978). Maser, Trappe and Nussbaum (1978) also report extensive feeding on fungi in northeast Oregon and northwest Colorado.

Fungi comprised the largest percentage in *Clethrionomys*' stomachs collected during the present study. Greater amounts of fungi were eaten in the control sites than in the burn sites where forbs became a more prominant item. In the TCB red-backed voles utilized an abundant forb (*Lupinus*), whereas in the DB they ate a rare forb (*Astragalus*). Decreased use of fungi in the burns may reflect a corresponding decreased availability of preferred fungi other than *Cenococcum geophilum*, the only fungal resource measured.

Additional studies are needed to begin to understand the interrelationships among small mammals, fungi, and reforestation. Spores of fungi are known to be viable after passing through the digestive tract of small mammals (Trappe and Maser 1976). This is probably an important dispersal mechanism for the fungi. The small mammal mycophagists may maintain their food source by inoculation of hypogeous fungi on host plants; thus, reforestation is enhanced as a result of the obligatory symbiotic relationship between mycorrhizal fungi and the conifers.

Peromyscus maniculatus

Substantial regional and seasonal variations in the diets of deer mice are known to occur and are reviewed in many articles. Large amounts of arthropods and seeds are consumed (Flake 1973; Hamilton 1941; and Williams 1959). Few studies have investigated the diets of deer mice on burned areas. Halford (1978) reported that on both burn and control sagebrush areas over 90% of the diets were of animal matter, with a predominance of coleopteran adults and lepidopteran larvae and little difference in diets between sites. Tevis (1956) also noted increased amounts of insects in the diets of deer mice from cut over areas in California, with seeds being more prevalent in the stomachs of deer mice from the forested areas. Fungi have been reported to vary in importance in the diets of deer mice. Hamilton (1941) reported little or no fungi in the diets of deer mice from eastern forests of United States while Maser, Trappe, and Nussbaum (1978) found fungi in 73% of the stomachs of deer mice in western Oregon. On a successional area in a coniferous forest, 22 years after a fire, Williams and Finney (1964) found the use of fungi (*Endogone* in particular) increased from a frequency of 43% in the first year studied to 92% during the second year.

In the present study arthropods were the most important food items in all the areas sampled. No consistent trends between burn and control sites were found due to a small sample size from the DC and large individual variations in types of arthropods eaten. Dipterans, hymenopterans, and lepidopterans made up the largest percentage of arthropods eaten; dipterans and hymenopterans were also common arthropods sampled in the areas. However, only small numbers of lepidopterans were collected in pitfall traps. Thus in some instances, the deer mice may be taking advantage of good supplies of certain arthropods for food, whereas in other cases they may be selecting preferred arthropods for foods.

More seeds were eaten in the DC than in the burn sites and may reflect a greater abundance and diversity of this food supply in the control site. Forbs were commonly found in the stomachs but were of low percentage density and varied little between the sites the first year. An increase in the amount of forbs eaten was recorded the second year in the DB and the TCB and may reflect an increase in this food supply due to an additional growing season.

Eutamias amoenus

Chipmunks tend to be omnivorous, with regional variations in diet reflecting food supply. Vaughan (1974) reports that *Eutamias* ate primarily seeds and arthropods in subalpine forests. Chipmunks of westcentral Colorado were dependent on the common dandelion for summer food (Carleton 1966). Fungi are also important items in the diets of chipmunks. Maser, Trappe, and Nussbaum (1978) found fungi frequently (82%) and in large quantities (50%) in the stomachs of chipmunks in Oregon. Tevis (1952, 1953) reported averages of 33-44% fungi by volume in stomachs of chipmunks in California.

The diets of the yellow-pine chipmunk from the two study areas in Yellowstone National Park suggested an opportunistic foraging strategy as there were site, year and individual variations. Generally, arthropods, seeds, fungi, and forbs were all important items in their diets, but there were major differences in use of these food types. In the DB, arthropods were the major food item in 1978 and were followed by forbs in importance. However, in 1979 arthropods and forbs were utilized equally. In the TCB fungi comprised the largest proportion of the diet during 1978, but were of minor importance in 1979 and were replaced by increased amounts of seeds and forbs. A suggested relationship existed in the TCC where a larger number of seeds were found and the greatest amount of seeds in the diet of *Eutamias* occurred. Also, chipmunks apparently took advantage of a good supply of *Arnica* found in the DB. Increased forb use by *Eutamias* during the second year may be related to increased amounts of vegetation after an additional growing season although no data were available to support this.

Small Mammal Composition

Under conditions following clearcutting it appears that a change in both species composition and abundance of small mammals occurs. Several investigators have reported increased numbers of deer mice and decreased numbers of red-backed voles on clearcut burns in conifer forests (Gashwiler 1970; Heath 1973; Martell and Radvanyi 1977; Sims and Buckner 1973; Tevis 1956). However, Kirkland (1977) found increased numbers of both *Peromyscus* and *Clethrionomys* following fires in mixed hardwood-conifer forests of northern Appalachia.

Under conditions of natural fires, in Minnesota, Krefting and Ahlgren (1974) also reported deer mice as the most abundant small mammal until after the 7th year, after which red-backed voles increased and became predominant. Similarly, in a short-term live trapping study in the DB and in the TCB in 1977, Caprio (1977) found that deer mice were the most abundant small mammals. Red-backed voles were only rarely captured.

In the present study snap-trapping results indicate the predominance of *Clethrionomys* in all sites. *Peromyscus* and *Eutamias* were more numerous in the burn sites than in the control sites. The abundance of *Clethrionomys* in the present study was inconsistent with other observations reported in the literature but may have resulted from better habitat available after the natural fires. Apparently, ample vegetation and log cover were available in 1978, and their nutritional and water requirements were met by fungal and forb resources present in the burns. Increased numbers of *Peromyscus maniculatus* and *Eutamias amoenus* following fire were not surprising. Both species are known to prefer open sites and disturbed areas rather than closed canopy forests. Their opportunistic feeding habits would allow them to take advantage of a variety of food resources in the burns. Some species, including *Tomiasciurus hudsonicus* and *Glaucomys sabrinus*, were apparently eliminated by the fire through the loss of habitat.

Although *Peromyscus* were present in the burn sites, they were not as abundant as other authors have found (Tevis 1956; Gashwiler 1970). Grant (1972) suggested that interspecific competition is extensive among rodents but lacked experimental demonstration under field conditions. He stated that interspecific competition between two species will be evident by inverse numerical relationships or inverse spatial relationships (habitat segregation). Several researchers have documented inverse numerical relationships among species of small mammals within a community. This has been the case between *Microtus montanus* and *Microtus pennsylvanicus* (Stoecker 1972; Koplin and Hoffmann 1968) and between *Microtus* spp. and *Clethrionomys gapperi* (Grant 1970; Clark 1973). However no study thus far has been able to show any response of *Peromyscus* to the presence of *Clethrionomys* (Grant 1970; Getz 1969). Removal studies of *Clethrionomys* in the DB site during the present study gave no conclusive evidence that numbers of *Peromyscus* were affected.

This study has attempted to describe the effects of natural fires on the small mammal communities in two coniferous forests of Yellowstone National Park. Studies such as this are necessary to help explain the processes involved in natural environments. The data collected can be used to supply evidence to decide whether current fire management policies are in keeping with the goals of maintaining a natural environment within the Park boundaries.

From the present study it is apparent that the community of small mammals has adapted to an environment susceptible to rapid changes after fires. Certainly, abundance data indicate that the small mammal community is not eliminated by fires. In fact, in some cases certain species increased in numbers. Food habits studies indicate that the small mammals are adaptable in their diets and thus exhibit a wide habitat tolerance in an environment that may change rapidly. Bendell (1974) suggested that the small mammals may actually help perpetuate burnable habitat through the presence of squirrel middens or nests in or beneath trees that may act as kindling during a lightning strike. These small mammals may also inadvertently aid in the revegetation of their habitat through seed distribution and inoculation of symbiotic fungal spores. Thus, short-term and long-term successional changes in composition and abundance of small mammals in natural burns are expected (Taylor 1973), and the overall diversity of the ecosystem is increased by a mosaic of burns of various ages.

REFERENCES CITED

Ahlgren, I. F. 1974. The effects of fire on soil organisms. In T. T. Kozlowski and C. E. Ahlgren (eds.), Fire and ecoystems. New York: Academic Press. pp. 47-72.

Bailey, A. W. and C. E. Poulton. 1968. Plant communities and environmental relationships in a portion of the Tillamook burn, Northwestern Oregon. Ecol. 49:1-13.

Barbour, M. G. and R. T. Lange. 1967. Seed populations in some natural Australian top soils. Ecol. 48:153-155.

Bendell, J. F. 1974. Effects of fire on birds and mammals. In T. T. Koslowski and C. E. Ahlgren (eds.), Fire and ecosystems. New York: Academic Press. pp. 73-138.

Calhoun, J. B. 1948. North American census of small mammals. Release No. 1 (Rodent Ecology Project, John Hopkins University). 8 p.

Caprio, T. 1977. Small mammals trapped on the Divide and the Trail Creek fires. Research report available from: Research Office, Yellowstone National Park, Mammoth, Wyoming. 6 pp.

Carleton, W. M. 1966. Food habits of two sympatric Colorado sciurids. J. Mammal. 47:91-103.

Clark, T. W. 1973. Local distribution and interspecies interactions in microtines, Grand Teton National Park, Wyoming. Great Basin Naturalist 33:205-217.

Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. Northwest Sci. 33:43-64.

Despain, D. G. 1972. Fire as an ecological force on Yellowstone ecosystems. Information Paper No. 16, Yellowstone National Park, Mammoth, Wyoming. 3 pp.

Flake, L. D. 1973. Food habits of four species of rodents on a short grass prairie in Colorado. J. Mammal. 54:636-647.

Fox, J. F. 1978. Forest fires and the snowshoe hare--Canada lynx cycle. Oecologia 31:349-353.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in westcentral Oregon. Ecol. 51:1018-1026.

Getz, L. L. 1968. Influence of water balance and microclimate on the local distribution of the red-backed vole and white-footed mouse. Ecol. 49:276-286.

__________. 1969. Laboratory studies of interaction between the white-footed mouse and red-backed vole. Can. Field Nat. 83: 141-146.

Gniadek, S. 1977. Some aspects of avian ecology following the 1974 Trail Creek and 1976 Divide Fires in Yellowstone National Park. Final research report available from: Research Office, Yellowstone National Park, Mammoth, Wyoming. 75 pp.

Grant, P. R. 1970. Experimental studies of competitive interaction in a two-species system. II. The behavior of *Microtus, Clethrionomys* and *Peromyscus*. Anim. Behav. 18:411-426.

__________. 1972. Interspecific competition among rodents. Ann. Rev. Ecol. Syst. 3:79-106.

Gullion, G. W. 1967. Factors affecting ruffed grouse populations in the boreal forests of northern Minnesota, U. S. A. Proc. 8th Int.Congr. Game Biol. 1967, Finn. Game Res. 30:103-117.

Halford, D. F. 1978. Repopulation and food habits of small mammals on a burned sagebrush desert. In Ecological studies on the Idaho National Engineering Laboratory site. Progress report available from: U.S. Dept. of Energy, Washington, D.C. pp. 200-206.

Hamilton, W. J., Jr. 1941. The food of small forest mammals in eastern U.S. J. Mammal. 22:250-263.

Heath, M. 1973. Small mammal populations in clearcuts of various ages in southcentral Montana. Unpublished Master's thesis, Montana State University, Bozeman. 33 pp.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Washington: Univ. of Washington Press. 730 pp.

Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. Ecol. 54:1111-1117.

Hurst, G. A. 1970. The effects of controlled burning on arthropod density and biomass in relation to bobwhite quail brood habitat on a right-of-way. Tall Timbers Conference on Ecological Animal Control by Habitat Management 2:173-183.

Jones, R. E. 1968. A board to measure cover used by prairie grouse. J. Wildl. Mgmt. 32:28-31.

Kirkland, G. L., Jr. 1977. Responses of small mammals to the clear cutting of northern Appalachian forests. J. Mammal. 58:600-609.

Koplin, J. R. and R. S. Hoffmann. 1968. Habitat overlap and competitive exclusion in voles (*Microtus*). Am. Midl. Nat. 80:494-501.

Krefting, L. W. and C. E. Ahlgren. 1974. Small mammals and vegetation changes after fire in a mixed conifer-hardwood forest. Ecol. 55: 1391-1398.

Martell, A. M. and W. F. Merritt. 1979. Preliminary trials of radio-tagging black spruce seed with Manganese-54 for seed fate studies. Canadian Wildlife Service Progress Notes No. 94. 4 pp.

Martell, A. M. and A. Radvanyi. 1977. Changes in small mammal populations after clearcutting of northern Ontario black spruce forest. Can. Field. Nat. 91:41-46.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal-small mammal interrelationships with emphasis on Oregon coniferous forests. Ecol. 59:799-809.

Merritt, J. F. and J. M. Merritt. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a subalpine forest. J. Mammal. 59:576-598.

Morrill, W. L. 1975. Plastic pitfall trap. Envir. Entomol. 4:596.

Radvanyi, A. 1970. Small mammals and regeneration of white spruce forests in western Alberta. Ecol. 51:1102-1105.

Raunkiaer, C. 1934. The life forms of plants and statistical plant geography; being the collected papers of C. Raunkiaer, translated into English by H. G. Carter, A. G. Tensley, and Miss Fausboll. Clanendon, Oxford. 632 pp.

Reichman, O. J. 1978. Personal communication: Letter on file with author. Research biologist with the Museum of Northern Arizona, Flagstaff, Arizona.

Reid, V. H., R. M. Hansen, and A. L. Ward. 1966. Counting mounds and earth plugs to census mountain pocket gophers. J. Wildl. Manage. 30:327-334.

Schloyer, C. R. 1977. Food habits of *Clethionomys gapperi* on clearcuts in West Virginia. J. Mammal. 58:677-679.

Sims, P. H., and C. H. Buckner. 1973. The effect of clear-cutting and burning of *Pinus banksiana* forests on the populations of small mammals in southeastern Manitoba. Amer. Midl. Natur. 90:228-231.

Snedecor, G. W. and W. G. Cochran. 1967. Statistical methods. Iowa: Iowa State Univ. Press. 593 pp.

Sparks, D. R. and J. C. Malechek. 1968. Estimating percentage dry weight in diets using a microscope technique. J. Range Manage. 21: 264-265.

Stoecker, R. E. 1972. Competitive relations between sympatric populations of voles (*Microtus montanus* and *Microtus pennsylvanicus*). J. Anim. Ecol. 41:311-329.

Taylor, D. L. 1973. Some ecological implications of forest fire control in Yellowstone National Park, Wyoming. Ecol. 54:1394-1396.

Tevis, L. P. 1952. Autumn foods of chipmunks and golden-mantled ground squirrels in the northern Sierra Nevada. J. Mammal. 33:198-205.

__________. 1953. Stomach contents of chipmunks and mantled squirrels in northeastern California. J. Mammal. 34:316-324.

__________. 1956. Responses of small mammal populations to logging of Douglas fir. J. Mammal. 37:189-196.

Trappe, J. M. 1964. Mycorhizal hosts and distribution of *Cenococcum graniforme*. Lloydia 27:100-106.

__________. 1969. Studies on *Cenococcum graniforme*. I. An efficient method for isolation from sclerotia. Can. J. Bot. 47: 1389-1390.

Trappe, J. M. and C. Maser. 1976. Germination of spores of *Glomus macrocarpus* (Endogonaceae) after passage through a rodent digestive tract. Mycologia 68:433-436.

Vaughan, T. A. 1974. Resource allocation on some sympatric subalpine rodents. J. Mammal. 55:764-795.

Williams, C. 1959. Food habits of the deer mouse. J. Mammal. 40: 415-419.

__________ and B. A. Finney. 1964. *Endogone*--food for mice. J. Mammal. 45:265-271.