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Small Mammals of the Bitterroot National Forest: A Literature Review and Annotated Bibliography

Dean E. Pearson

Abstract

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Small mammal literature from western Montana and the Northern Rocky Mountains was reviewed to assess the ecological role of small mammals on the Bitterroot National Forest of western Montana and in the Northern Rocky Mountains. The goal was to understand how small mammals relate to succession and how proposed ecosystem management goals would affect small mammals, the predators they support, and the roles they play in forest ecosystem functions. Small mammals fulfill numerous important roles in forest ecosystems by supporting a wide range of predators, dispersing seeds and mycorrhizal spores, altering the composition of vegetative communities through herbivory and seed predation, and preying on insects. Coarse woody debris (CWD) is among the most important habitat components for forest small mammals. Guidelines are suggested for managing CWD for small mammals with an emphasis on CWD recruitment.

Keywords: small mammals, coarse woody debris, Montana

The Author

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Contents

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PART I - LITERATURE REVIEW

Introduction

The purpose of this literature review is to:

1) identify the small mammals of the Bitterroot National Forest;
2) determine their habitat associations with regard to moisture, elevation, and successional gradients;
3) outline the ecological importance of the various taxa; and
4) determine the possible outcome of land management practices on composition and abundance of the small mammal communities and the potential effects of changes in the small mammal communities on the ecosystem as a whole.

To this end, an examination and review of the relevant literature on small mammals is presented here with an annotated bibliography of the more pertinent local and regional research.

In 1993, the Bitterroot National Forest (BNF) initiated the Bitterroot Ecosystem Management Research Project (BEMRP). This project applies an ecosystem-level multi-disciplinary approach to research and management on the BNF. The primary goal of BEMRP is to restore an ecosystem, altered by fire suppression and timber harvest, to a more natural state and in so doing reduce the potential for catastrophic fire by favoring natural, low-intensity ground fires.

Low- to mid-elevation habitats on the BNF were historically dominated by dry seral ponderosa pine (*Pinus ponderosa*) and moist seral ponderosa pine-western larch (*Larix occidentalis*) stands. Open understories in these fire-dependent, savanna-like forests were maintained in presettlement times by frequent, low-intensity fires (Arno 1976). One-hundred years of fire suppression and timber harvest practices have encouraged dense stands of Douglas-fir (*Pseudotsuga menziesii*) and grand fir (*Abies grandis*) within the under- and midstories and, in some cases, the canopy. Overcrowded stand conditions and the ensuing competition for limited resources has increased the susceptibility of stands to disease and insect infestations. With this buildup in the under- and midstory, which contributes to the fuel loads and provides a fire ladder to the canopy, the stage is set for catastrophic fires. Because low-elevation ecosystems of the BNF are adapted to a low-intensity, high-frequency fire regime (Arno 1976), intense fires may deleteriously affect these habitats. Catastrophic fires obviously lead to undesirable consequences in the urban interface. Recent development adjacent to the BNF has pushed the urban interface beyond the dry, seral ponderosa pine habitat of the lowest elevations into more heavily forested cover types that are more susceptible to intense fires.

The subalpine zone has been similarly impacted. At high elevations, the fire-dependent whitebark pine (*Pinus albicaulis*) community has been weakened by encroaching subalpine fir (*Abies lasiocarpa*), and outbreaks of mountain pine beetle (*Dendroctonus ponderosa*), and white pine blister rust (*Cronartium ribicola*) (see Arno and Hoff 1989). Unique plant-animal interactions render this an important community for the Clark's nutcracker (*Nucifraga columbiana*) and the grizzly bear (*Ursus arctos*) (Hutchings and Lanner 1982; Kendall 1981; Tomback 1981). Furthermore, whitebark pine is restricted to high elevation sites and so persists only within a narrow range of abiotic and biotic conditions (Arno and Hoff 1989).

By reintroducing periodic, low-intensity fire and variously applying knowledgeable thinning and harvesting methods, researchers and managers wish to 1) re-establish fire-dependent, park-like ponderosa pine and ponderosa pine-western larch communities to presettlement conditions in mid- and lower elevation sites; 2) stabilize high-elevation, whitebark pine communities; and 3) reduce the threat of insect infestation, disease, and catastrophic fire on the BNF.

Re-establishing historic ecosystem functions to the Bitterroot watershed will result in local and landscape-level changes in vegetation that will strongly affect existing animal communities. To incorporate wildlife into the BEMRP framework, a Faunal Research Group was appointed to study the BNF's wildlife populations. Research has been initiated on bird and mammal communities to understand how animals fit into historic dynamics of the BNF ecosystem and how they will respond to changes proposed in BEMRP management strategies.

In recognition of the importance of small mammals in forest ecosystems, the BEMRP Faunal Research Group, led by L. Jack Lyon, sponsored an exploratory research project to investigate the effects of timber harvest and fire on small mammal community composition and abundance (Landres et al. 1995). After an initial field season in 1994, the group found that more extensive long-term research than time and funding would permit was necessary to answer the questions posed. However, the questions were important enough for a group to begin reviewing the current scientific literature in order to assess the role of proposed fire and timber management practices on composition and abundance of small mammals on the BNF.

In keeping with the goals of BEMRP, this report presents an ecosystem-level review of small mammals by elaborating on their ecological interactions on the BNF and within the Northern Rockies. The role that mycophagous rodents play as catalysts for mycorrhizal symbiosis is critical to forest ecosystem function and so receives critical attention. The trophic importance of small mammals as "prey-base" is similarly developed, though somewhat less so, since this aspect of interaction has been addressed to a limited extent from the carnivore perspective in other recent literature reviews (Ruggiero et al. 1994; Heinemeyer and Jones 1994; Weaver 1993; Butts 1992a, 1992b). Finally, the central position of coarse woody debris (CWD) in linking predator with prey and fungi with fungivore is examined in light of an ecosystem management perspective.

Small mammals and habitats reviewed in this document are present throughout the Northern Rocky Mountains, and ecological interactions and habitat relations discussed here are generalizable throughout most of this region. Additionally, many of the ecosystem management principals being applied within the BNF will also be applied to much of the Northern Rocky Mountains via the Columbia River Basin Project. This information is therefore pertinent to most if not all National Forests within Region 1 of the United States Forest Service.

Region of Literature Search

The intent of this project was to review small mammal studies conducted on the BNF and in areas within the Northern Rocky Mountain Region that fulfilled the criteria of being similar in habitat and physiographic attributes to those habitats found on the BNF. The extent of research conducted on small mammals within the BNF was found to be extremely limited. Therefore, ecological information addressing small mammals occurring on the BNF was acquired primarily from research in the Northern Rocky Mountains and secondarily the Pacific Northwest. For rare species and species under-represented in the ecological literature within these regions, review included pertinent information from regions beyond the northwestern United States.

Defining Small Mammals

The term small mammals is used to describe a variety of taxa that fulfill the criteria of being both "small" and mammals. Although the term is widely used, it provides little information without clearly defining the range of taxa being discussed. Table 1 presents a species list for small mammals occurring on or suspected of occurring on the BNF based on surveys conducted within the Bitterroot Valley and review of species distributions published in the literature. Information made available by the Montana Natural Heritage Program substantially augmented this species list. The list in Table 1 serves to identify species recognized in this literature review as the small mammals of the BNF. Species not included due to the terrestrial focus, as outlined in the criteria set forth for this review, include the beaver (*Castor canadensis*) and the muskrat (*Ondatra zibethica*). Small carnivores (Carnivora) are similarly excluded, except to the extent of mention in predator-prey interactions. Bats (Chiroptera) and snowshoe hares (*Lepus americanus*) are, for ecological reasons, not generally recognized as members of the more traditional suite of small mammals (see Chew 1976). However, the snowshoe hare is included because of its importance as prey-base, and in some cases, forest pest. Bats are also included because of their ecological importance as insect predators and their high degree of sensitivity to disturbance.

Forty-one species are listed in Table 1. The volume of literature surrounding these species, even when geographically delimited to the northwestern United States, is tremendous. Although searches of data bases were extensive, as evidenced by the literature cited section, they could by no means be exhaustive. However, within the realm of the primary focus of this review (the response of small forest mammals to timber harvest), the literature presented is virtually exhaustive for this region. Many similar studies have been conducted in the eastern United States and Canada that are, for numerous ecological reasons, not included here. Most of these have been reviewed elsewhere (Pearson 1994; Kirkland 1990).

Characteristics of Small Mammals Affecting Ecological Interactions

Small mammals are an extremely diverse group of organisms representing a variety of ecological guilds.

Table 1—Small mammals of the Bitterroot National Forest. Common names and former scientific names for species are presented in Appendix 1. Nomenclature follows Jones et al. (1992). Global and state rankings and United States Fish and Wildlife Service and United States Forest Service status are given as reported in the Montana Natural Heritage Program Element Occurrence database for the spring of 1995 (Montana Natural Heritage Program, Helena, MT).

Species	Presence	Rank		Status	
		Global	State	USFWS	USFS
Cinereus shrew	p	G5	S5		
Preble's shrew *	p	G4	S3	C2	
Vagrant shrew	p	G5	S4		
Montane shrew	p	G5	S5		
Water shrew	p	G5	S5		
Pygmy shrew	s	G5	S4		
Dwarf shrew *	s	G4	S3		
Little brown myotis	p	G5	S5		
Yuma myotis **	p	G5	S3	C2	
Long-eared myotis	p	G5	S4	C2	
Fringed myotis *	p	G5	S3	C2	
Long-legged myotis	p	G5	S4	C2	
California myotis	p	G5	S4		
Eastern small-footed myotis	p				
Western small-footed myotis	s	G5	S4	C2	
Silver-haired bat	p	G5	S4		
Big brown bat	p	G5	S4		
Hoary bat	s	G5	S4		
Spotted bat *	s	G4	S1	C2	sen
Townsend's big-eared bat *	p	G4	S2S3	C2	sen
Pika	p	G5	S5		
Snowshoe hare	p	G5	S5		
Columbian ground squirrel	p	G5	S5		
Richardson's ground squirrel	p	G5	S5		
Golden-mantled ground squirrel	p	G5	S5		
Yellow-pine chipmunk	p	G5	S5		
Red-tailed chipmunk	p	G5	S5		
Red squirrel	p	G5	S5		
Northern flying squirrel	p	G5	S4		
Northern pocket gopher	p	G5	S5		
Idaho pocket gopher	p	G4	S3		
Deer mouse	p	G5	S5		
Bushy-tailed woodrat	p	G5	S5		
Northern bog lemming	p	G4	S2		sen
Heather vole	p	G5	S5		
Southern red-backed vole	p	G5	S5		
Meadow vole	p	G5	S5		
Montane vole	p	G5	S5		
Long-tailed vole	p	G5	S5		
Water vole	p	G5	S4		
Western jumping mouse	p	G5	S5		

* species of special concern as determined by the Montana Natural Heritage Program
** watch list species as determined by the Montana Natural Heritage Program
p: present on BNF; confirmations are based on museum specimens, literature review, review of surveys conducted on the BNF, or sightings or trapping conducted by the author.
s: suspected of residing on BNF, based on distribution records and habitat affiliations.
G1 or S1: species critically imperiled because of extreme rarity ([5 occurrences).
G2 or S2: species imperiled at the global or state level, respectively, because of rarity or biological factors rendering it very vulnerable to extinction (6-20 occurrences).
G3 or S3: species very rare or local throughout its range or found locally within a restricted range (21-100 occurrences).
G4 or S4: species apparently secure though it may be rare in parts of its range.
G5 or S5: species demonstrably secure though it may be rare in parts of its range.
C2: category 2; current information indicates that proposing to list as endangered or threatened is possibly appropriate, but insufficient biological information exists to warrant immediate listing.
sen = sensitive: "sensitive" as outlined by the Endangered Species Act.

They include insectivores (shrews and bats), fungivores (northern flying squirrel), omnivores (deer mice and red-backed voles), herbivores (voles, pikas), and granivores (chipmunks). Species also represent semi-aquatic (water shrews), fossorial (pocket gophers), terrestrial (most) and arboreal (tree squirrels) habits. The great diversity of the species collectively referred to as small mammals poses a challenge in terms of reviewing the ecological roles they play in the variety of environments they inhabit. However, a few important generalizations can be made about small mammals which, in the gross sense, bind them together ecologically and justify a collective review of this diverse array of taxa.

R-Selected

Most small mammals are r-selected. That is to say they produce large litters which mature quickly with little parental care (bats are the exception). The Muridae, mice and voles, are seasonally polyestrous and may produce up to 3 litters in a single year (Krebs and Meyers 1974). Several species produce litters during the winter when resources and conditions permit. In some microtine rodents, the first litter of the year matures and produces a litter of its own within the same season when conditions are optimal (Krebs and Meyers 1974). The result of this productivity is an abundance of biomass available for harvest by predators.

Surface-Area-to-Volume Ratios and Winter Survival Strategies

Small mammals have high surface-area-to-volume ratios that result in excessive heat loss, leaving them inordinately susceptible to hypothermia. This physiological condition greatly affects the ecology of small mammals living in the northern temperate zone. Physiological adaptations that evolved in response to cold include hibernation and torpor. Hibernation is a long-term depression of metabolic activity and body temperature in response to cold-related stress. In hibernation, body temperature approximates that of ambient temperature, just above freezing (usually within a den or cavity) (Schmidt-Nielsen 1975). Torpor also involves a reduction in metabolic activity and body temperature, but it usually lasts only a short time and body temperature drops only a few degrees, down to 10 to 20 °C (Wang 1989; Hudson 1978). Both are means of surviving periods of low resource availability and cold temperatures, and both affect activity patterns of temperate zone small mammals. This is particularly important with regard to the temporal availability of small mammals to predators (see Prey-Base section below).

Ironically, the smallest mammals, those most affected by high surface-area-to-body ratios, do not hibernate. The exception is the western jumping mouse (*Zapus princeps*) (Luoma 1970). Animals not hibernating must resort to behavioral strategies to survive extreme winter conditions. Many temperate zone rodents hoard food in anticipation of resource limitations in the winter. Pikas (*Ochotona princeps*) produce massive haystacks by drying herbaceous plants and flowers collected from the edge of talus slopes and caching them beneath boulders (Millar and Zwickel 1972). Northern pocket gophers (*Thomomys talpoides*) store foods in hypogeous and subnivian chambers (Tryon 1947). Deer mice (*Peromyscus maniculatus*), chipmunks (*Tamias* spp.), and red squirrels (*Tamiasciurus hudsonicus*) cache seeds (Pierce and Vogt 1993; Hatt 1943; Gordon 1943).

Shrews (*Sorex* spp.), which are at the theoretical lower size limit for homeothermy (Pearson 1948), employ a variety of behavioral and morphological tactics to survive the cold, including communal nesting (Davis and Joeris 1945), food caching (Martin 1984), and decreasing body mass over winter to reduce energy requirements (Mezhzherin 1964). Communal nesting has also been described for deer mice (Millar and Derrickson 1992). Many bats (Chiroptera) migrate to warmer climates and are unique among mammals in this respect. Other small mammals periodically enter torpor during winter, especially during inclement weather.

Winter survival strategies affect ecosystem dynamics by directing small mammal interactions with ecosystem components. Hoarding and caching behaviors often result in territoriality, which affects social structure and population dynamics of small mammals and their dispersion within habitats. These factors, in turn, regulate their abundance and temporal and spatial availability to predators. Seed predation can be heavy in some circumstances, but caching may result in seed dispersal when caches are forgotten (Abbott and Quink 1970; Radvanyi 1970; West 1968). In the case of the red squirrel, middens associated with caches and feeding areas function as important resting sites, denning sites, and access points to the subnivian zone for American marten (Ruggiero et al. in prep.; Ruggiero et al. 1998; Sherburne and Bissonette 1993; Buskirk 1984). Red-backed voles appear to be more abundant near squirrel middens suggesting that middens may also provide important resources for these voles (Ruggiero and Pearson in prep.). Hibernation reduces the number of species and individuals and thereby the total biomass available to carnivores during periods when environmental stress is greatest. These characteristics and their resulting impacts are discussed in greater detail later.

Ecological Role of Small Mammals in Forest Ecosystems

Small mammals consume little net primary productivity (NPP) in forest ecosystems. On the Hubbard Brook Experimental Forest in New Hampshire the three most abundant small mammals, the deer mouse, the southern red-backed vole, and the woodland jumping mouse, consume 0.3 percent of the aboveground NPP (Potter 1974). Energy utilization by small mammals in spruce forests (*Picea* spp.) has been estimated at 1.4 to 2.2 percent NPP (Grodzinski 1971; Hansson 1971). In general, NPP ingested by small mammals in forest ecosystems is less than 0.5 percent (see Potter 1976). Potter (1976) argues that use of NPP does not effectively assess the impact that small mammals have on forest ecosystems since much of the primary productivity in forests ends up in woody biomass (over 50 percent in Hubbard Brook [Whittaker et al. 1974]) and within the canopy, where it is unavailable to small mammals.

Although small mammals affect NPP only slightly, the specificity of their diets and high reproductive rates provide them with a means to greatly impact various aspects of ecosystem dynamics. Selective foraging by northern pocket gophers (*Thomomys talpoides*) for preferred forbs can affect species composition of local meadows and grasslands (Laycock and Richardson 1975). Pikas can significantly alter the composition of vegetation bordering talus slopes by selective foraging within a restricted swath surrounding such areas (Huntly 1987; Huntly et al. 1986). Shrews may function as keystone predators increasing diversity of insect communities by depredating the dominant insect species in the community (Anderson and Folk 1993), and deer mice and short-tailed shrews can control economically important insect pests through functional and numerical responses to prey increases (Holling 1959). Early research on forest small mammals arose due to concerns over their impact as seed predators (Tevis 1956a, 1956b) but has more recently recognized the potentially positive role small mammals play in mycorrhizal spore dispersal (Maser et al. 1978; Fogel and Trappe 1978). Perhaps the most prominent role of small mammals in community ecology is that of prey base supporting many carnivore species.

Seed Predation

Much of the early research on forest small mammals was conducted because of concerns that rodents deleteriously affect conifer regeneration by consuming conifer seeds (Gashwiler 1967, 1965; Tevis 1956a, 1956b; Squillace 1953; Adams 1950). Rodent seed predators in the Northern Rocky Mountains include red squirrels, chipmunks, deer mice, and southern red-backed voles (Radvanyi 1973, 1970; Schmidt and Shearer 1971; Adams 1950). Of these, red squirrels, which specialize in harvesting conifer seeds, are the most effective seed predator within forest stands (Smith 1970; Hatt 1943; Yaeger 1937). Red squirrels have an advantage over terrestrial rodents because they harvest cones before seed dispersal occurs. In northwest Montana, red squirrels removed as much as 82 percent of the ponderosa pine seed crop from a study site in 1965, but the average for 3 years was 44 percent (Schmidt and Shearer 1971). Smith (1970) contends that selective foraging by red-squirrels affects a variety of cone characteristics including number of seeds per cone, the time when cones shed seeds, the thickness of seed coats, and annual fluctuations in volume of cone crops. He concludes this selective pressure has resulted in a co-evolutionary relationship between conifers and squirrels. Deer mice may be the second most important conifer seed predator (Sullivan 1979a; Gashwiler 1979; Radvanyi 1973; Abbott 1961). They are generally the primary small mammal predator of seeds that reach the forest floor (Schmidt and Shearer 1971; Adams 1950). Both red squirrel and deer mouse population fluctuations have been correlated with changes in conifer seed crops (Halvorson and Engemen 1983; Gashwiler 1979; Schmidt and Shearer 1971).

When seed predation in forests is presented as a percentage of total mast consumed, the percentages are generally relatively small (Potter 1976), and when the potential population of seeds has been examined, seed abortions account for 70 percent of the total seed loss, red squirrels 14 percent, and other small mammals and birds 2 percent (Schmidt and Shearer 1971).

The effect that rodent seed predation may have on stand composition is unclear, but evidence may suggest that small mammals do influence tree biology. For example, the phenomenon of mast fall may have evolved in response to seed predation in an "attempt" to saturate predators in space and time so that sufficient seeds would survive to germinate. Such asynchronous fluctuations in populations of seed predators and mast are likely to result in many seeds surviving predation during years when small mammal populations are low and seed production is high (Potter 1976). Seedling survival studies have shown that survival was inversely proportional to seed germination (Hett 1971). Rodent seed predation during mast years could therefore function to thin seeds and bring about an increase in successful germination due to decreased competition for nutrients. Caching behavior exhibited by red squirrels, chipmunks, deer mice, and southern red-backed voles can result in seed dispersal when unused or forgotten caches germinate (Abbott and Quink 1970; West 1968; Tevis 1953).

These caches sometimes contribute significantly to tree recruitment. West (1968) concluded that 15 percent of ponderosa pine regeneration at his central Oregon study site originated from rodent caches, and Tevis (1953) suggested that the yellow-pine chipmunk (*Tamias amoenus*) was an important factor affecting natural stand regeneration in northeastern California. Severity and length of winter are presumably unpredictable. Evolution should therefore favor "over-achievement" among hoarding species. Ideally, stores will last into the spring, and as new crops mature they should be nutritionally and palatably preferable to last year's caches. This phenomenon would likely result in unused seed caches except in years of severe conditions when all caches are exhausted.

However, in intensively managed stands where manual seeding occurs, chipmunks and deer mice may deleteriously affect seeding efforts (Radvanyi 1973, 1970; Gashwiler 1967). This situation may be exacerbated if structure is removed through piling and burning of logging slash, since structure may provide "hiding" places for seeds. Radvanyi (1970) determined that approximately 50 percent of radiotagged spring-placed white spruce (*Picea glauca*) seeds were consumed within four months of placement. Krauch (1936) suggested that fire after logging aided stand regeneration by decimating populations of seed eating rodents, but Tevis (1956b) provided conclusive evidence that slash burning increased deer mice (the primary seed predator) populations on recent clearcuts. Other studies have also demonstrated increases in deer mice populations on burned clearcuts (Hooven and Black 1976; Hooven 1969).

Under these circumstances, timing of seeding is an important factor in reducing seed predation. Radvanyi (1970) observed that winter-placed radiotagged seeds exhibited 19 percent loss to predation whereas 50 percent loss was reported for spring-placed seeds. However, he observed a 5- to 6-fold increase in germination of winter-placed over spring-placed seeds and suggested that other factors, such as availability of moisture, are at least equally important in increasing germination rates following winter seeding. Supplemental feeding is another technique shown to reduce seed predation by deer mice in intensively managed stands (Sullivan 1979b).

Though rodents consume large numbers of conifer seeds (Sullivan 1979a; Radvanyi 1973, 1970; Schmidt and Shearer 1971; Adams 1950), no evidence was found that small mammal seed predation negatively affects natural forest regeneration. In fact, seed predation may increase seedling survival by reducing site competition (Hett 1971). Granivorous rodents may greatly reduce the number of manually placed seeds in clearcuts, and the more heavily managed a stand, the more important rodent seed predation may be, since alternative foods will be scarce. Supplemental feeding and later-winter seeding reduce seed predation by deer mice (1979b). These methods are more effective than pest control measures which often fail (see Malloy 1981; Sullivan 1979a).

Direct Effects on Trees

Debarking of trees and destruction of seedlings by porcupines (*Erithizon dorsatum*), snowshoe hares (*Lepus americanus*), red squirrels, and northern pocket gophers are also means by which small mammals may alter primary productivity and stand composition in forests (Sullivan and Klenner 1993; Sullivan and Sullivan 1988). These activities are more prominent early in stand development in intensively managed systems (for example, Sullivan and Moses 1986).

Herbicide campaigns (Borrecco 1976) and mechanical habitat destruction (Sullivan and Moses 1986) have been carried out to reduce snowshoe hare numbers in young conifer plantations in Washington and British Columbia. In the case of mechanical habitat destruction, even though populations of snowshoe hares were reduced, impact on trees by hares was not. However, Sullivan and Sullivan (1988) reported snowshoe hare damage to crop trees decreased as did hare populations after thinning of lodgepole pine stands in British Columbia. For red squirrels, Sullivan and Klenner (1993) found that supplemental feeding significantly reduced tree damage without increasing resident squirrel populations. They concluded this was an effective method of reducing bark damage in young lodgepole pine (*Pinus contorta*) stands.

Although supplemental feeding and timber treatments can minimize the impact of forest pests, encouraging natural predators such as lynx, fishers, martens, weasels, hawks, accipiters, and owls may be the most ecologically sound means of reducing the impact of these potential pests.

Insect Predation

Shrews and deer mice are prominent insect predators (Pearson et al. in review; Pearson in press; Frank 1967; Buckner 1958) that can control prey populations of important forest pests such as the pine sawfly (*Neodiprion sertifer*), at least up to saturation densities (Holling 1959). Platt and Blakley (1973) found higher diversity of arthropod prey positively correlated with abundance of the cinereus shrew (*Sorex cinereus*). They postulated that the shrew functioned as a keystone predator by suppressing populations of otherwise numerically dominant species in the community (but see Mills et al. 1993 for critique of keystone concept). A 2-year exclosure study by Andersen and Folk (1993) indicated that shrews and deer mice could reduce survival of acorn weevils (Coleoptera: Curculionidae), an important forest pest.

Field research on deer mouse predation of gall flies (*Urophora* spp.) released as biological control agents to reduce the spread of spotted knapweed (*Centaurea maculosa*) in westcentral Montana suggested that deer mice consumed between 150 and 250 larvae per mouse per night during winter in knapweed-infested grasslands (Pearson et al. in review; Pearson in press). Estimated numbers of gall fly larvae depredated per individual per month was 8058 in 1997 based on the nightly foraging potential of this species (Pearson in press). However, Pearson et al. (in review) argued that these data, based on snap trapping methods, underestimated true predation rates by as much as five-fold based on results from feeding trials that showed mice could consume an average of >1200 larvae per mouse per 24 hr interval. Deer mouse capture rates increased linearly in response to increasing knapweed cover (which translates to increasing gall fly densities), and mice were able to reduce their handling time when depredating seedheads by somehow assessing the likelihood that a seedhead contained larvae (Pearson et al. in review). Deer mice may affect some control over gall fly populations through these functional and numerical responses. Though the implications of such predation on this introduced biological control agent are not yet fully understood, the predatory potential of the deer mouse on insects is well illustrated by this example.

Few studies have addressed the potentially critical role small mammals may play as natural biological controls over forest insect pests, but this may be an important aspect of small mammal interactions within forest ecosystems.

Mycophagy and Spore Dispersal

Most higher plants maintain an obligatory symbiotic relationship with 1 or more species of mycorrhizal (root-inhabiting) fungi in order to meet their minimum nutrient requirements for survival (Marks and Kozlowski 1973; Sanders et al. 1975). Hypogeous forms of mycorrhizal fungi include Ascomycetes (truffles), Basidiomycetes (false truffles), and Phycomycetes (Endogonaceae); these groups make up a large and important component of the mycorrhizal community. Sporocarps of hypogeous fungi are belowground and so do not have access to wind for spore dispersal as do epigeous (aboveground) forms. These fungi are therefore dependent upon animals for spore dispersal, and Maser et al. (1978) suggest that small mammals are the primary vectors for dissemination of their spores.

Mycophagy (fungus consumption) has been described for numerous species of small mammals throughout North America (Maser et al. 1978; Fogel and Trappe 1978). In many cases, mycophagy is incidental or opportunistic, but several species including the northern flying squirrel (*Glaucomys sabrinus*) and western red-backed vole (*Clethrionomys californicus*) consume fungi almost exclusively and show a strong preference for hypogeous forms (Maser et al. 1985; Maser et al. 1978; Hayes et al. 1986). In consuming fungal sporocarps, small mammals also incidentally ingest and thereby disperse ecologically important microorganisms such as yeast and nitrogen-fixing bacteria (Li et al. 1986a).

Available information suggests a long evolutionary relationship exists between small mammal mycophagists and hypogeous mycorrhizal fungi. Hypogeous fungi emit distinctive odors that attract small mammals (Fogel and Trappe 1978; Maser et al. 1978). These odors may be analogous to odors and coloration in flowers that have evolved to lure pollinators. Although many epigeous fungi also emit strong odors, hypogeous fungi predominate in samples of small mammal digestive tracks (Maser et al. 1978). Howard et al. (1968) established that deer mice locate hypogeous sporocarps through olfaction. Species like the northern flying squirrel and red-backed voles, which specialize on mycorrhizal fungi, are presumably even more adept at finding sporocarps using olfactory cues. Fogel and Trappe (1978) note that hypogeous sporocarps do not emit an odor until they are mature. This would prevent sporocarps from being found and consumed before spores are ready for distribution and is arguably a coadapted evolutionary trait. The correlation noted by some investigators (Fogel and Trappe 1978; Tevis 1953) between rodent size and the size of sporocarps ingested suggests that species of fungi producing small sporocarps may require smaller animals such as voles, mice, shrews, or insects to disperse their spores, since these are the only species for which consumption of these tiny sporocarps is nutritionally and energetically beneficial.

Spores of mycorrhizal fungi, yeast, and nitrogen-fixing bacteria are viable after passing through rodent digestive tracts (Kotter and Farentinos 1984; Li et al. 1986a; Trappe and Maser 1976), and the probability that spores will reach fertile substrates may increase through mycophagy, since mycophagist rodents forage where sporocarps are likely to be found. Li et al. (1986b) found the feces of northern flying squirrels and Douglas' squirrels (*Tamiasciurus douglasii*) to be as effective a medium as yeast extract in promoting growth and nitrogenase activity in nitrogen-fixing bacteria collected from the feces. Kotter (1981) determined that tassel-eared squirrels (*Sciurus aberti*) disseminated 200 million to 1 billion fungal spores per gram of fecal material in Colorado ponderosa pine communities, implying great dispersal potential for some mycophagist rodents.

Table 2 presents information for species on the BNF for which mycophagy has been documented. Much of the information comes from Maser et al. (1978) who give an extensive review of mycophagy for rodents in the Pacific Northwest. Fogel and Trappe (1978) provide comprehensive lists of fungi consumed by fungivores and of mycophagists that consume fungi as reported in the literature. These two papers are key works on mycophagy, and both are included in the annotated bibliography.

Although many species of small mammals are known to consume hypogeous mycorrhizal fungi, the extent that a species relies on fungi is quite variable, and some species are probably more important than others as disseminators of mycorrhizal spores (Table 2). In the northern Rocky Mountain Region, the northern flying squirrel and the southern red-backed vole are likely the primary and secondary mycophagists, respectively. Chipmunks may also be important, and the red squirrel may play a variable though less certain role. The deer mouse is best described as an opportunistic mycophagist, but its ability to switch habitats may make it a critical bridge for dispersal of spores from late successional forests to newly disturbed habitats. The literature is reviewed for the primary mycophagist species below, followed by a discussion and some speculation (resulting from gaps in the literature on mycophagy for this region) on the probable roles of mycophagist rodents in ecosystems on the BNF.

The northern flying squirrel is possibly the most specialized fungivorous rodent in North America and is probably the strongest mycophagist in the Northern Rocky Mountain Region. Maser et al. (1978) found hypogeous fungi made up 78 percent of the stomach contents by volume of 12 individuals captured in Oregon coniferous forests. More recently, Maser et al. (1985) reported the mean volume of fungi in stomachs of 21 individuals collected during the summer in northwestern Oregon was 100 percent. Approximately 80 percent of this volume was hypogeous fungi. The remaining portion was unidentified fungi. The stomach contents of an additional 61 individuals caught throughout the year in northeastern Oregon resulted in 93 percent fungi by volume, of which lichens made up 60 percent and hypogeous fungi made up 11 percent, on average; epigeous and unidentified fungi made up the remaining contents. In northeastern California, for 24 northern flying squirrels captured throughout the year, nearly 100 percent of the stomach contents by volume contained fungi (McKeever 1960). On average, 51 percent of the volume was sporocarps and 49 percent was lichen. In

Table 2—Summary of mycophagy information for small mammals occurring on the Bitterroot National Forest. The absence of a species from the list indicates no volumetric information was available for that species in the Northwest, but absence does not preclude it as a mycophagist.

Family and species	% volume	Type	n	State	Author citation
Ochotonidae					
Pika	8	hyp	10	OR	Maser et al. 1978
Sciuridae					
Yellow-pine chipmunk	50	hyp	11	OR	Maser et al. 1978
	38		39		Tevis 1952
	28		170		Tevis 1953
Red squirrel	77	hyp	5	OR	Maser et al. 1978
Northern flying squirrel	78	hyp	12	OR	Maser et al. 1978
	90-100	hyp	82	OR	Maser et al. 1985
Geomyidae					
Northern pocket gopher	1	epi	11	OR	Maser et al. 1978
Muridae					
Deer mouse	trace	hyp	21	OR/NV	Maser et al. 1978
	10	hyp	62	BC/OR	Maser et al. 1978
Bushy-tailed woodrat	10	hyp	34	OR	Maser et al. 1978
Red-backed vole	72		10	OR/CO	Maser et al. 1978
	5-100	hyp		WY/CO	Williams and Finney 1964
Montane heather vole	60	hyp	1	OR	Maser et al. 1978
			11	CO	Williams and Finney 1964
Long-tailed vole	28	hyp	4	OR	Maser et al. 1978
Western jumping mouse	100	hyp	1	WY	Williams and Finney 1964
		hyp	3	CO	Williams and Finney 1964

hyp = hypogeous
epi = epigeous

general, northern flying squirrels rely heavily upon hypogeous sporocarps most of the year, but in winter and at times when sporocarp production is down, they consume lichens (Maser et al. 1985; Maser et al. 1978; McKeever 1960). In central Idaho, northern flying squirrels consumed predominantly lichens and fungi with lichens most abundant in winter diets and fungi most abundant in summer (Rosentreter et al. 1997). The only other item in stomachs was vascular plant tissue in 25 percent of 2000 samples.

In the Pacific Northwest, the western red-backed vole vies with the northern flying squirrel for the role of primary mycophagist. The southern red-backed vole replaces this species in the Rocky Mountain states both geographically and in terms of its place as a prominent mycophagist rodent. Ure and Maser (1982) observed diets of southern red-backed voles to contain over 90 percent fungal sporocarps in eastern Oregon and approximately 60 percent fungus in western Washington. Gunther et al. (1983) also reported high frequencies of fungus and lichen (= 77 percent relative frequency for animals from clearcuts and forest) in stomachs of southern red-backed voles in the Cascade Mountains of western Washington.

Food habit studies of the southern red-backed vole have been conducted throughout much of North America (see Pearson 1994 for review), but research on food habits of this vole in the Northern Rocky Mountains is limited, and mycophagy is not well addressed. Maser and Maser (1988) reported that 27 *Clethrionomys gapperi idahoensis* consumed approximately 46 percent fungi by volume of which around 19 percent was hypogeous sporocarps. They found 16 stomachs of the subspecies *C. g. galei*, also from the Rocky Mountain region, contained 45 percent fungi by volume of which about 18 percent was hypogeous. These same 2 subspecies were found by Maser et al. (1978) to have consumed 72 percent fungi by volume, wherein 75 to 95 percent was hypogeous fungi. Clark (1973) examined 25 voles from Grand Teton National Park, Wyoming, but did not include a category for fungi, although he indicated that 26 percent of the volume of stomachs was unidentified. He reported 59 percent of the contents was plant material. Ten of 27 individuals from Colorado and Wyoming had consumed hypogeous Endogone, but volumetric and relative frequencies of fungi in stomachs were not determined (Williams and Finney 1964).

Maser and Maser (1988) examined stomach contents of red-backed voles collected across the United States and concluded that habitat was a more important factor in determining extent of mycophagy than was taxonomic status. In the Northern Rocky Mountains, the southern red-backed vole's diet is approximately 45 percent fungi with around 20 percent being hypogeous (Maser and Maser 1988). However, Maser and Maser (1988) is the only good food habit study reporting on the volume of fungi found in stomachs of the southern red-backed vole in the Northern Rocky Mountains, and most information on hypogeous sporocarp production comes from the Pacific Northwest (Amaranthus et al. 1994; Luoma 1991; Luoma et al. 1991; Fogel and Hunt 1979; Fogel 1976; but see Harvey et al. 1976 for MT).

Other fungivorous small mammals in the Rocky Mountains may be seasonal or opportunistic mycophagists. Tevis (1952, 1953) showed that yellow-pine chipmunks in northern California rely heavily on hypogeous fungi. In northeastern Oregon, Maser and Maser (1987) reported that stomach contents of 135 individuals consisted of about 13 percent hypogeous fungi by volume.

Beg (1969) did not report fungi in the diets of either red-tailed chipmunk or yellow-pine chipmunk in western Montana, but he examined only cheek pouch contents of live-captured individuals. It is likely that cheek pouches are biased toward cached foods such as seeds which Beg found a preponderance of in his samples. Hypogeous fungi would probably be consumed upon collection. Beg indicated that on several occasions he observed both species feeding on "something" gathered beneath loose bark of old trees and stumps. He also often observed them foraging in the leaf litter. Both locations are likely spots for fungi.

No studies of chipmunk mycophagy in this region were found, so it is difficult to draw conclusions, but chipmunks may consume and disperse spores of hypogeous fungi here in important quantities. Fungus in the diet of the deer mouse is highly variable, depending presumably on sporocarp availability (which is known to be seasonally abundant in spring and fall) (Luoma 1991; Luoma et al. 1991).

The importance of a species as a vector for mycorrhizal spores varies depending on habitat requirements, diet, and the behavior of other mycophagous species in the community. Habitat and dietary specialists like the northern flying squirrel and the southern red-backed vole facilitate spore dissemination within forest stands. By specializing on mycorrhizal fungi and being restricted to later successional stages (Pearson 1994; Witt 1992; Nordyke and Buskirk 1991; Scrivner and Smith 1984; Andersen et al. 1980), they are likely the primary catalysts for mycorrhizal symbiosis within moist forests in the Northern Rocky Mountains.

However, these species rarely enter newly disturbed sites, and the hot, dry conditions associated with recent clearcuts and stand-replacing fire are believed to destroy mycorrhizal fungi (Clarkson and Mills 1994; Maser et al. 1978). Yet the obligatory nature of mycorrhizal symbiosis requires that the symbionts be present for the survival of newly germinating trees, creating an apparent ecological dilemma for non-wind dispersed hypogeous species. Habitat and dietary generalists such as deer mice may function as vectors for re-introducing spores to early seral conditions. Deer mice do not specialize on mycorrhizal fungi, but a given individual, having indulged itself in an opportunistic meal of sporocarps, may carry hundreds of thousands of spores from the forest into an adjacent clearcut or burn, thereby facilitating the reintroduction of critical mycorrhizal fungi into a habitat devoid of mycobionts for regenerating trees. Until recently the deer mouse had been regarded only as seed predator (Tevis 1956a). Such a limited understanding of the ecological role of this species may undermine the success of long-term forest ecosystem management.

Chipmunks may consume larger quantities of sporocarps and do so more often than deer mice. Although they are more specialized in their use of habitats than deer mice, they may also bridge the ecotone separating recently cut or burned sites from mature forest. The yellow-pine chipmunk prefers ponderosa pine savanna, but it is also found in shrubby habitats associated with early seral conditions and forest edges (see Habitat Associations).

The lack of literature on hypogeous fungi and small mammal mycophagy in the northern Rocky Mountain Region leads to much speculation regarding the relative importance of different mycophagist species in different habitats; however, mycophagy, and therefore mycophagist rodents, clearly play an important part in forest ecosystem functions within this region.

Prey-Base

The Northern Rocky Mountains accommodate a rich assemblage of predators, most of which occur on the BNF. Small mammals are the trophic substrate upon which many of these predators depend for survival during at least some portion of the year. Red-backed voles, *Microtus* spp., red squirrels, and snowshoe hares are particularly important prey within forested environments. The removal of any one of these species could significantly alter upper trophic levels. Red-backed voles are the primary food source for American marten (*Martes americana*) (Buskirk and Ruggiero 1994; Weckwerth and Hawley 1962) and boreal owls (*Aegolius funereus*) (Hayward et al. 1993) in the Northern Rocky Mountains. Snowshoe hares are a critical resource for fisher (*Martes pennanti*) in the Cabinet Mountains, western Montana (Roy 1991). The 10-year cycle linking snowshoe hare and lynx (*Lynx lynx*) populations is well documented in northern latitudes (Koehler and Aubry 1994; Keith 1963). Keith and Cary (1991) have also shown that weasels (*Mustela frenata* and *M. erminea*) and mink (*M. vison*) exhibit a 10-year cycle that is synchronous with that of lynx in Alberta suggesting that they also may take advantage of the snowshoe hare resource. Snowshoes are also taken, to a lesser extent, by marten and wolverine (*Gulo gulo*) (see Buskirk and Ruggiero 1994; and Banci 1994).

Microtus spp. are the primary prey for grassland predators (Ryszkowski et al. 1973; Golly 1960), but they also occur in restricted habitats in forest environments where they are one of the few species of small mammals present in marten diets in greater proportions than they occur in surrounding habitats (Buskirk and Ruggiero 1994).

Red squirrels are the primary prey of northern goshawks in Wyoming, where they occurred in 55 percent of 900 goshawk pellets (Squires in prep.). Red squirrels occur in the diets of marten but rarely make up >10 percent of the diet (see Buskirk and Ruggiero 1994). Since distribution, abundance, and seasonal availability do not greatly affect marten access to red squirrels, the under-representation of red squirrels in marten diets could indicate that they have difficulty securing squirrels due to their larger size. However, marten are capable of killing snowshoe hares (Weckwerth and Hawley 1962), which are much larger than squirrels, and snowshoe hares comprise a large proportion of their diets in southeastern Manitoba (Raine 1987).

Buskirk and Ruggiero (1994) suggested a symbiotic relationship may exist between red squirrels and martens, wherein squirrels provide important resting sites, denning sites, and access to the subnivian space in the form of middens (Ruggiero et al. in prep.; Ruggiero et al. 1998; Sherburne and Bissonette 1993; Buskirk 1984). They argued red squirrels may benefit marten by creating critical marten habitat, and the two species may coexist at midden sites. For example, Buskirk (1984) reported that 70 percent of his Alaska marten rest sites occurred within red squirrel middens even though red squirrels occurred in only 5 percent of 467 scats and colon tracts collected from the same area concurrent to the study. Red squirrel middens may also be favorable feeding sites for marten, since middens appear to have higher numbers of red-backed voles than non-midden sites (Ruggiero and Pearson in prep.).

Insights Into Prey Selection—Food habit studies of marten indicate that they generally take prey items in proportion to their availability (Buskirk and Ruggiero 1994; Weckwerth and Hawley 1962). Results of an intensive study in Idaho suggests this is also true for boreal owls (Hayward et al. 1993). This is likely the result of cost effective foraging within the predators' primary habitat, as has been described for long-eared owls (*Asio otus*) (Korpimaki 1992). The red-backed vole is the most common species encountered by both predators throughout the year and is consumed in proportion to its availability. This does not negate its importance as a food item, but rather explains its importance to forest carnivores in terms of their cohabitation within structurally complex environments.

Boreal owls and marten do exhibit selection for some prey. Marten show a "preference" for *Microtus* spp., and boreal owls consume a disproportionate amount of northern pocket gophers during years of low red-backed vole abundance. This prey selectivity may result from optimal foraging strategies (see Pyke et al. 1977). Within the moist coniferous forest habitat occupied by both predators, the aforementioned prey are habitat-specific and clumped in their distributions. *Microtus* favor grass-forb openings in the forest and grass-forb areas along riparian corridors (Kinsella 1966; see Habitat Associations). Northern pocket gophers occupied a wider range of habitats within Hayward et al.'s (1993) study area including sage, lodgepole pine, and wet meadows, but this species favors microsites with deep, moist soils and leaves conspicuous sign indicating its presence. These characteristics allow predators to develop search images (Pietrewics and Kamil 1979) for microsites where prey are concentrated. Additionally, these species weigh more than the "non-selected" red-backed vole. Mean adult weights for these three prey items in Idaho were: red-backed vole, 27 g; *Microtus* spp., 30 g; northern pocket gopher, 101 g (Hayward et al. 1993). Selection for the northern pocket gopher by boreal owls and *Microtus* by marten can probably be explained by the higher probability of success associated with foraging for a clumped and predictably located resource and the greater energetic returns associated with capturing larger prey.

The underrepresentation of deer mice in marten diets (Buskirk and Ruggiero 1994) and their apparent underrepresentation in boreal owl diets is also congruent with optimality theory. Deer mice are present in essentially all habitats (see Habitat Associations), are less predictable in their selection of microhabitats (Pearson 1994) and weigh less than red-backed voles, 24.2 g for adults (Hayward et al. 1993). Predation on deer mice is probably opportunistic due to low returns and the lack of predictability associated with finding them. However, in winter, deer mice are believed to undergo prolonged periods of torpor and have been shown to reduce activity at this time (Kucera and Fuller 1978; Fuller et al. 1969). As a result, their availability is reduced in winter and this may not be accounted for in some food habits studies. The small size of shrews may partly explain their rarity in the diets of marten (Buskirk and Ruggiero 1994) and other carnivores (Jackson 1961), but these animals also have pungent scent glands that may render them less than palatable. Shrews are, however, a common prey item in boreal owl diets (Hayward et al. 1993).

Hibernation and Seasonal Availability of Prey—Seasonality of the temperate zone environment affects other aspects of prey availability. Hibernation by chipmunks, ground squirrels, and jumping mice greatly reduces their accessibility to predators over the winter months as is apparent from winter food habit studies of forest carnivores (see Ruggiero et al. 1994). Other small mammals such as northern pocket gophers become generally unavailable within tunnels beneath the snow pack (Hayward et al. 1993). This places a heavy burden on small mammals that do not hibernate and especially on those that make use of the snow surface. Although marten forage beneath the snow, they probably depend largely on subnivian spaces near woody debris (Sherburne and Bissonette 1994, 1993). Therefore, use of the subnivian space provides some refugia from predation.

When animals leave the subnivian space, they greatly increase their susceptibility to predation. Deer mice, red-backed voles, *Microtus* spp., and shrews are active both on the snow and within the subnivian space (Kucera and Fuller 1978). These species are correspondingly more important in the diets of forest carnivores during winter. Shrews are more abundant in the diets of fisher than expected (Powell and Zielinski 1994) given their general absence from most carnivores' diets (Jackson 1961). Fishers may prey upon shrews more because fishers are restricted to the snow surface by their large size. Shrews make heavy use of the snow surface (pers. obs.) and forage more frequently during the winter than in the summer (Gillihan 1992). Although deer mice also travel across the surface, they reduce their activity in the winter and are suspected of periodically entering torpor (Kucera and Fuller 1978; Fuller et al. 1969). Red squirrels and northern flying squirrels remain active and accessible all winter (see Foresman in review). Red-backed voles and northern flying squirrels increase in the diets of boreal owls (Hayward et al. 1993) in the winter, and red-backed voles and red squirrels are often the most important species in diets of marten at this time (Buskirk and Ruggiero 1994).

Most hibernating species are associated with early-seral stages (ground squirrels, chipmunks, and jumping mice) whereas late-seral stands support species that do not hibernate (tree squirrels). *Microtus* associated with early successional stages are subject to radical population fluctuations while their late-seral counterpart, the red-backed vole, is much more stable from year to year. This condition should result in late-seral forests being favored by predators in winter due to a greater abundance of accessible food and perhaps in general due to greater stability over time. However, predators capable of using recent clearcuts and grasslands might be expected to shift their efforts to these areas in spring when ground squirrels appear and in years when *Microtus* populations peak to provide a superabundant prey.

Red-backed Voles, American Marten, and the Role of CWD—Coarse woody debris is an important habitat feature for both predators and prey in forest ecosystems. Red-backed voles favor mature and old-growth forest in the Northern Rocky Mountains (Pearson 1994; Nordyke and Buskirk 1991; Scrivner and Smith 1984; Halvorson 1982; Ramirez and Hornocker 1981). Pearson (1994) and Nordyke and Buskirk (1991) determined that old-growth characteristics and CWD predicted macrohabitat selection (selection at the stand level) of the southern red-backed vole. Pearson (1994) also established a direct link between southern red-backed voles and the use of CWD at the microhabitat level. In comparing data collected from red-backed vole trap sites with data from randomly selected trap stations, Pearson (1994) observed that southern red-backed voles were more closely associated with larger diameter logs in some stands and younger decay classes in others. Using fluorescent pigment tracking to identify exact patterns of movement, Pearson determined that voles used logs as travel corridors through the forest.

Marten are known to associate primarily with mature forest at the macrohabitat scale (Buskirk and Ruggiero 1994), and forests exhibiting old-growth characteristics may provide optimal habitat (Buskirk and Powell 1994). Studies of resting site ecology and use of the subnivian space for foraging suggest that CWD and snags are important microhabitat components for marten (Sherburne and Bissonette 1994; Taylor and Buskirk 1994; Sherburne and Bissonette 1993; Buskirk et al. 1989; Buskirk 1984). Resting sites associated with CWD are critical to marten when ambient temperatures drop below a critical threshold (Taylor and Buskirk 1994). Squirrel middens may serve a similar role to that of CWD in marten resting site ecology by providing an insulating surface superior to that afforded by snow alone (Sherburne and Bissonette 1993; Buskirk 1984). Access to the subnivian space via CWD is also crucial for foraging (Sherburne and Bissonette 1994).

However, conclusions drawn by Sherburne and Bissonette (1994) that marten select subnivian access points based upon some assessment of small mammal biomass beneath the snow may be premature. Their use of spring trapping data to indicate small mammal abundance near CWD may be misleading. However, small mammals are known to aggregate within the subnivian space by shifting away from areas used in summer (West 1977), and studies conducted during the snow-free period indicate that small mammals shift use areas seasonally (for example, Belk et al. 1988; Vickery 1981). Coarse woody debris likely creates a more extensive subnivian space that may afford better access to resources and therefore be preferred by small mammals (Coulianos and Johnels 1962; as cited in Merritt and Merritt 1978). However, use of CWD sites has been shown to change between spring and summer (Belk et al. 1988) and may change between spring and winter as selection criteria change. During snow-free periods, CWD sites may function as foraging areas for truffles (Clarkson and Mills 1994), or may be chosen for hiding or escape cover. In winter, other less well understood aspects of subnivian ecology may drive selection for such sites. The correlation observed by Sherburne and Bissonette (1994) is one between marten winter access points and spring abundance of small mammals and should not be extrapolated beyond this.

It remains to be seen whether marten are selecting sites for small mammal abundance or for some criteria that small mammals are similarly selecting. Unless martens tunnel, which is unlikely as a general strategy, they require larger spaces beneath the snow for foraging such as those associated with CWD. Larger spaces may be favored by small mammals for more expansive foraging areas or better ventilation, since carbon dioxide is likely to accumulate beneath the snow.

If winter aggregation in small mammals is a cold adapted behavior as suggested by West (1977), small mammals may aggregate in small inaccessible subnivian pockets where moss is abundant. They could then be least available to marten, which are restricted to larger spaces, when cold-related stress is highest. This factor could affect the temporal availability of subnivian small mammals and should be considered before drawing conclusions about marten selection of access points based upon spring small mammal densities.

Coarse woody debris may play a seasonally dynamic role in predator prey relationships in the Northern Rocky Mountains. In winter, CWD serves to link predator and prey via portals which facilitate interchange between the subnivian space and the snow surface. During snow-free seasons, CWD may provide prey with refugia in space and time from predators, thereby potentially dampening oscillations in predator-prey cycles (see Huffaker 1958 and Gause 1934). Wolff (1980) maintains that habitat heterogeneity afforded by mosaics of thick, low evergreen and deciduous vegetation provides refugia for snowshoe hare populations in Alaska. He argues that reduced cyclicity in more southern populations is due to increases in generalist predators and alternative prey species that allow prey switching and dampen oscillations. Lee (1995) has shown that vagrant shrews were more stable on sites with CWD than on controls lacking this structural component.

Southern red-backed voles exhibit multiannual fluctuations in some populations, but not in others.

Habitat heterogeneity has been implicated in determining population stability within this genus (Bondrup-Nielsen and Ims 1988). Bondrup-Nielsen and Ims (1988) suggest that habitat heterogeneity dampens oscillations by preventing habitat space from being filled, thereby precluding social interactions and other intrinsic population control mechanisms that could initiate a crash, but they ignore the role of predation in this interaction. However, their hypothesis does not exclude predation, and others argue that predation is important in dampening prey cycles (Erlinge et al. 1983). The habitat heterogeneity hypothesis as presented by Bondrup-Nielsen and Ims (1988) is more probable when predation is introduced into the equation as demonstrated by laboratory studies (Huffaker et al. 1963; Huffaker 1958; Gause 1934).

That CWD may stabilize ecosystem processes by dampening oscillations in red-backed vole populations seems quite possible. If CWD does play such a role, whether it does so by means of prey refugia, habitat heterogeneity, or both remains to be seen. In any case, microhabitat selection by forest carnivores and their small mammal prey indicates CWD is an important component in the ecology of these species.

Source and Sink Populations

An understanding of the nature and dynamics of source and sink populations (Pulliam 1988; Van Horne 1983) is extremely important for managing small mammals and for understanding how habitat quality for small mammals relates to habitat quality for predators and predator-prey interactions. Differences in productivity combined with social controls such as territoriality result in some habitats giving rise to source populations, populations which produce beyond the local carrying capacity, and others functioning as sink populations (unsustainable populations where mortality exceeds natality).

Sink populations have been identified in the Northern Rocky Mountains (Pearson 1994) and possibly in the central Rocky Mountains (Nordyke and Buskirk 1991) for the southern red-backed vole. A lack of old-growth attributes such as CWD was associated with sink populations in young lodgepole pine stands studied by Nordyke and Buskirk (1991) in Wyoming. In Glacier National Park, Pearson (1994) similarly determined that young lodgepole pine stands were sinks and further suggested that some stands that were over 350 years old might also be sinks based on a combination of population parameter estimates.

Populations of southern red-backed voles within lodgepole pine stands were identified by Pearson (1994) as dispersal sinks based on a lack of breeding adults. However, other sink populations identified by Pearson (1994) and Nordyke and Buskirk (1991) for southern red-backed voles and by Sullivan (1979c) for deer mice were associated with moderate to high densities of animals, and so required detailed population demographic information to distinguish them as dispersal sinks. For species such as the southern red-backed vole that function as prey-base for a variety of predators and fulfill other important ecological roles such as spore dispersal (see Mycophagy and Spore Dispersal), it is important to recognize that abundance is not always a good indication of habitat quality (Van Horne 1983) and that superficially similar habitats may not be equally productive. Management that supports productive small mammal populations will best provide for predator populations and spore dispersal activities.

Rare and Sensitive Small Mammals

Bats

Seven of 13 species of bats known to occur or suspected of occurring on the BNF are potential candidates for listing under the Endangered Species Act, pending further biological information (Category 2) (Table 1). Townsend's big-eared bat (*Plecotus townsendii*) and the spotted bat (*Euderma maculatum*) are recognized as "Sensitive" species by the USDA Forest Service. However, the spotted bat may not occur on the BNF. Of the species known to occur on the BNF, Townsend's big-eared bat is listed as imperiled within the state (S2), and the yuma myotis (*Myotis yumanensis*) and fringed myotis (*Myotis thysanodes*) are listed as very rare in Montana (S3). The eastern small-footed myotis (*Myotis leibii*) is not currently recognized as present within the state by the Montana Natural Heritage Program, so no status is given. However, this species does occur in Montana where it is perhaps most abundant in the Bitterroot Valley (Hoffmann et al. 1969b) and should probably be listed as S3 or S2 at the state level.

There are several reasons for the precarious status of such a large proportion of bats. Understanding these will help to understand how bats can be protected on the BNF. In general, bats are extremely sensitive to disturbance in hibernation and maternity roosts (Genter 1989; Humphrey and Kunz 1976). Therefore, when hibernacula and maternity colonies are too often disturbed, sites are abandoned and whole colonies may perish if individuals are unable to reestablish themselves in available, undisturbed habitat. Townsend's big-eared bats are very sensitive to disturbance in maternity colonies, and Humphrey and Kunz (1976) conclude that disturbance could threaten the survival of colonies. Disturbance of big brown bats

(*Eptesicus fuscus*) at maternity roosts in British Columbia reduced site fidelity and decreased reproductive success (Brigham and Fenton 1986). Given the specificity of site selection for roosts exhibited by many species, and the energetic demands of mammalian flight which further requires that roosting sites be located near feeding sites, many bats are probably limited by a unique combination of foraging site and roosting site conditions.

Surveys should be conducted on the BNF to identify hibernacula and maternity roosts. Once these sites are identified, they can be protected from management and recreational disturbance. Because roost sites are often point locations such as caves or mine adits within other habitats (for many bats), they are relatively easy to manage by grating off entrances to adits or caves. This also reduces the potential for human injury in these locations.

Large old trees provide important habitat for tree roosting bats and maternity colonies for some species and so should also be managed with this in mind. Thomas and West (1991) reported that in Washington and Oregon, bat activity in old-growth stands was 2.5 to 9.8 times greater than in younger stands and concluded that large decayed trees in old growth provided critical roosting habitat. Since large ponderosa pine snags are recognized as important sites for some species in British Columbia (Brigham 1991), proposed management of ponderosa pine stands on the BNF as outlined in BEMRP reports may favor some bat fauna. Nonetheless, additional efforts will be necessary to maintain this diverse component of the BNF small mammal community.

Pygmy Shrew

The pygmy shrew (*Sorex hoyi*) is currently ranked as G5 and S4 with the Montana Natural Heritage Program. In Idaho, it is a species of special concern, and in Wyoming, it is a Priority 2 species (see Foresman 1989). The pygmy shrew is rare in the state, and its presence on the BNF is not yet confirmed. However, it has been captured nearby in Idaho subalpine fir (*Abies lasiocarpa*) and grand fir (*Abies grandis*) stands (Foresman 1986) and is very likely present on the BNF.

The pygmy shrew seems capable of surviving a wide range of moisture and seral conditions (see Habitat Associations). This species has been collected in clearcuts in Montana (Brown 1967a) as well as from disturbed floodplains (Key 1979) and so may not respond deleteriously to timber harvest practices. A general lack of knowledge regarding ecology and distribution precludes management recommendations for this species.

Dwarf Shrew

The dwarf shrew (*Sorex nanus*) is the smallest mammal in North America (Foresman 1989). This species is found most commonly in rocky habitats at high elevations in Montana (see Habitat Associations). The dwarf shrew has not been reported on the BNF, but its distribution and habitat associations indicate that pitfall trapping may produce specimens in high-elevation rocky habitats. Due to its rarity in Montana and in North America, this species is listed by the Montana Natural Heritage Program as a species of special concern that is globally secure though rare (G4) and very rare at the state level (S3) (Table 1). Because of its habitat affiliations, the dwarf shrew is unlikely to be affected by most management activities on the BNF.

Preble's Shrew

Preble's shrew is a rare shrew of arid sage (*Artemisia* spp.) habitats and has been reported only once in the Bitterroot Valley in 1910, 8 miles northeast of Stevensville (Hoffmann and Fisher 1978). The area described has likely changed a great deal since 1910, and the population that existed may have been extirpated by development. Habitat associations described for Preble's shrew (see Habitat Associations) suggest that other populations may exist in sagebrush habitats within the foothills on the BNF. Pitfall trapping of the sage community for this species might prove fruitful. Snap trapping and Sherman live trapping of this community might also produce other new records of rare species known to occur in similar habitat in adjacent Beaverhead County (see Hoffmann et al. 1969a). Preble's shrew (*Sorex preblei*) is classified by the Montana Natural Heritage Program as a species of special concern that is globally secure though rare (G4) and very rare within the state (S3) (Table 1).

Northern Bog Lemming

The northern bog lemming (*Synaptomys borealis*) occurs at the southern extent of its range in Montana. This species is considered a Pleistocene relict and is found in association with bog and fen habitats that are themselves relict communities surviving in isolated pockets within the state. The northern bog lemming is more common in northern latitudes, but even there its populations are localized, and its avoidance of traps has limited ecological information on this species to anecdotal accounts and speculation. For these reasons, this species is listed by the Montana Natural Heritage Program as globally secure though rare (G4) and as imperiled at the state level (S2) (Table 1). The USDA Forest Service recognizes this microtine as a "Sensitive" species within this region.

The fact that the northern bog lemming has persisted for some 10,000 years since the late Pleistocene in isolated habitats is testimony to its long-term viability. However, the human factor adds a new dynamic to this equation. Reichel and Beckstrom (1994) identified threats to this species as cattle grazing and trampling within bog/fen habitats, and timber harvest around such habitats where the species is present. They provide guidelines for protection of these habitats.

However, there is reason to question whether bog lemmings are actually restricted to bog/fen habitats. Pearson has taken 2 specimens in association with mesic old-growth stands near streams as a result of incidental captures while trapping for other species (McDonald Creek, Glacier National Park and Big Creek, BNF, unpublished data). Since surveys by Reichel and Beckstrom (1994 1993) and Pearson (1991) targeted bog/fen habitats, their results cannot be used to infer that bog lemmings favor bog habitats. Other potential habitats (such as cedar and spruce old-growth near streams) must be trapped with equal effort before any such conclusions can be drawn. However, their relative success in capturing bog lemmings in bog/fen systems implies some association exists. I suggest the assumption that bog lemmings require "bog" habitats is reasonable based on current information (Reichel and Beckstrom 1994, 1993; Pearson 1991). Any management or other activity that might alter bog or fen habitats could jeopardize the persistence of this unique species. Bogs and fens are defined by their hydrology and associated acidity (see Mitsch and Gosselink 1986) and bog/fen plant communities and, therefore, possibly bog lemmings are dependent upon these hydrological conditions. Any activity likely to alter bog/fen hydrology (forestry, grazing, trampling, road or trail building, etc.) may destroy the unique flora and fauna associated with these rare communities.

This species has been identified at 2 sites on the BNF: Meadow Creek (Reichel and Beckstrom 1993) and Big Creek (D. E. Pearson, unpublished data). Additional surveys could be conducted at minimal expense to determine the distribution of northern bog lemmings on the BNF. This would be the first step in managing for this rare, sensitive species on the BNF.

Habitat Associations

Shrews

Five species of shrews have been identified on the BNF: the cinereus shrew (*Sorex cinereus*), the montane shrew (*S. monticolus*), the water shrew (*S. palustris*), Preble's shrew (*S. preblei*) and the vagrant shrew (*S. vagrans*). Preble's shrew is represented by only one specimen within the Bitterroot watershed (Hoffmann and Fisher 1978). The pygmy shrew has not been identified on the BNF, but one was taken nearby in Idaho, and this species is likely present on the BNF (Foresman 1986). The dwarf shrew is not known from the BNF but has been found in high-elevation rocky habitats in the Northern Rocky Mountains including the isolated mountain ranges of the Sweetgrass Hills and Bearpaw Mountains, Montana (Brown 1967a; Hoffmann and Taber 1960; Thompson 1977). This shrew may also occur on the BNF, which has an abundance of such habitat near the species' current range.

The vagrant shrew and the montane shrew are closely related and morphologically very similar. This similarity has resulted in some confusion regarding the taxonomic status of these shrews. In western Montana and the Northern Rocky Mountains, morphology of the two species converges to such an extent that mammalogists could not distinguish between them (Hennings and Hoffmann 1977), and Findley (1955) lumped them together into a single species: the vagrant shrew. More recently, Hennings and Hoffmann (1977) have reinstated full species status and clarified the differences between the 2 species.

This distinction is important not only for identification of these shrews in the field, but also for interpreting the literature surrounding them. In early papers, *S. obscurus* = *S. monticolus*. After Findley's 1955 review of the taxonomy, distinctions were no longer made between the 2 species except by authors who maintained their separation at the subspecies level. In such cases, *S. vagrans vagrans* = *S. vagrans*, and *S. vagrans obscurus* = *S. monticolus*. Clothier (1955) refers to *S. vagrans monticola,* which is presumably *S. monticolus*. According to Hennings and Hoffmann (1977), shrews identified as *S. vagrans* by Brown (1967a), Spencer and Pettus (1966), Ingles (1961), and Hoffmann and Taber (1960) are all *S. monticolus*. Further interpretation of the literature requires careful reading and examination of range maps provided for these species by Hennings and Hoffmann (1977). Overall, a good deal of data regarding habitat associations of *S. vagrans* and *S. monticolus* was lost where subspecies were not assigned and confused where taxonomy was misused.

Live vagrant, cinereus, and montane shrews can often be identified in the field using a hand lens by determining the position of the medial tines on the upper front incisors relative to the pigmentation line (pers. obs.; Hennings and Hoffmann 1977). Other field characteristics reportedly can also be used: tail length, pelage color, odor (in breeding males), robustness of the rostrum, and number of callosities on the hind toes (Van Zyll de Jong 1982; Hawes 1977; Hennings and Hoffmann 1977). Collected specimens are generally easy to identify in the lab, and the cinereus shrew is easily separated from vagrant and montane shrews based on relative length of the third unicuspid (Hoffmann and Pattie 1968). Field biologists studying small mammals need not lump shrews into *Sorex* spp. thereby losing valuable information. The Montana mammal key, *A Guide to Montana Mammals* (Hoffmann and Pattie 1968), does not distinguish between vagrant and montane shrews. The keys in Foresman (in review), Hennings and Hoffmann (1977) or Jung and Hoffmann (1981) should be consulted to distinguish between these species.

The cinereus shrew, the vagrant shrew, and the montane shrew are the most common shrews in western Montana. The cinereus shrew has the widest distribution of any North American shrew (Hoffmann and Pattie 1968), and the montane shrew is more widely distributed than the vagrant shrew, which is restricted to areas within the Pacific Northwest and the Rocky Mountains (see maps in Hennings and Hoffmann 1977). Hoffmann and Pattie (1968) reported that the vagrant shrew was more common than the cinereus shrew in western Montana, but since it is now evident that they combined vagrant and montane shrews, it is unclear how abundance of the three species compare for this area. In mature and old-growth forests of Glacier National Park, where the three species are sympatric, the montane shrew is comparatively rare (K. A. Keating, unpublished data). In mature grand fir forests on the University of Montana Biological Station, Flathead Lake, vagrant shrews made up 56 percent, cinereus shrews 35 percent, and montane shrews 9 percent of captures for the three species (McCracken 1990). Hoffman (1960) similarly found vagrant shrews most abundant followed by cinereus and montane shrews within the cedar-hemlock zone of Washington and Idaho. Spildie (1994) reported a preponderance of vagrant shrews (85 percent of two species) captured in Grand Teton National Park. However, shrews identified as vagrant shrews were montane shrews (see Hennings and Hoffmann 1977; and discussion above).

Clothier (1955) trapped shrews in Glacier National Park, at Yellow Bay on Flathead Lake, and near Missoula. He reported extensive overlap between *S. vagrans monticola* (=*S. monticolus*) and *S. cinereus* but always found *S. monticolus* four times more abundant. Williams (1955) found *S. cinereus* and *S. obscurus* (=*S. monticolus*) sympatric within moist habitats in Colorado as did Smith (1988) in Alberta. In Washington, Terry (1981) concluded that *S. vagrans* inhabited alder stands and sites with a high water table, but was rare in closed forest. He caught *S. monticolus* in forested habitats in microsites associated with surface debris, but not mineral soil. Hawes (1977) conducted an intensive study of *S. vagrans* and *S. obscurus* (=*S. monticolus*) in 40-year-old western red cedar (*Thuja plicata*) and western hemlock (*Tsuga heterophylla*) stands in British Columbia. Distribution patterns indicated strong habitat separation between the vagrant and montane shrews. The montane shrew selected mossy sites beneath hemlock on mor soils, and the vagrant shrew favored the more mesic habitats under cedar on less acidic modor soils, where sword fern (*Polystichum munitum*) provided understory cover.

Although habitat separation was distinct over several generations of shrews and was clearly important, Hawes (1977) observed that territorial boundaries separating species near habitat interfaces matched boundaries of neighboring individuals more closely than lines dividing habitats. He concluded that interspecific interactions were important in maintaining ecological separation between vagrant and montane shrews. He suggested that odors emitted via the dermal glands of reproductively active males, which are sufficiently distinct to identify the two species in the field, may function as a reproductive isolating mechanism between species (Hawes 1976, 1977).

Few studies identify habitat or microhabitat separation between the vagrans complex, montane, and cinereus shrews in the Northern Rocky Mountains, though many variously describe their habitats as wet or moist sites (Spencer and Pettus 1966; Clothier 1955), and as noted above, extensive overlap is reported. Spencer and Pettus (1966) observed extensive overlap between *S. vagrans* (=*S. monticolus*; see Hennings and Hoffmann 1977) and *S. cinereus* in Colorado. However, they felt they identified an area of separation between the two species. They concluded that the cinereus shrew was more abundant in a shrubby patch of marsh than was the montane shrew and suggested that 1) this might result from a founder affect or 2) true habitat segregation was observed, but the discriminating variables could not be discerned. Hoffmann and Pattie (1968) described the cinereus shrew as the more xeric species and suggested that it is excluded from wetter sites by vagrant shrews when sympatric. However, Brown (1967a) determined that the cinereus shrew was found in relatively wetter sites (moist bogs) than *S. vagrans* (=*S. monticolus*; see Hennings and Hoffmann 1977) in the central Rocky Mountains of Wyoming, regardless of elevation. The relatively drier sites described by Brown (tree and shrub communities, and rock slides) where montane shrews outnumbered cinereus shrews were also structurally more complex than the mesic sites. It may have been this attribute that montane shrews were selecting for, since as Brown (1967a) reported, moisture did not vary greatly among sites.

McCracken (1990) studied habitat use by vagrant, montane, and cinereus shrews on two plots, one termed "wet" the other "dry," at the University of Montana Biological Station on the east shore of Flathead Lake. Sixty-two percent of 82 vagrant shrews inhabited the wet plot, while 78 percent of 51 cinereus shrews used the dry plot. Only 13 montane shrews were captured. Of these 13, 69 percent were from the dry plot and 31 percent from the wet. The vagrant shrew was significantly closer to water and was associated with greater abundance and density of logs >7.5 cm diameter than the other species. Cinereus shrews were captured in areas higher in woody stem densities than vagrant shrews. Montane shrews were captured too few times to draw conclusions about habitat use. Habitats used by vagrant shrews on the University of Montana Biological Station plots were both wetter and structurally more complex than those inhabited by cinereus shrews. Given its cosmopolitan distribution, the cinereus shrew expresses a wider ecological amplitude than the other two shrews and may be excluded from more mesic and/or more structurally complex habitats by vagrant and montane shrews. Hoffman (1960) captured vagrant, cinereus, and montane shrews within drier habitat types of the cedar-hemlock zone but caught only the vagrant shrew in the wettest habitat types trapped.

In an attempt to determine the upper elevational limit of shrews, Clothier (1955) sampled in the 1800- to 2000-m zone in Glacier National Park. Having no success at this elevation, he inferred that the upper elevational limit for shrews in this area was around 1800 m based on captures by Bailey (1918) and Jackson (1928) within the 1524- to 1829-m zone. However, Hoffmann and Taber (1960) caught four *S. vagrans* (=*S. monticolus*; see Hennings and Hoffmann 1977) on Logan Pass (2012 m), seven on the Beartooth plateau, WY (3048 m) and four in the Crazy Mountains, MT (3048 m). Brown (1967a) captured *S. vagrans* (=*S. monticolus*; see Hennings and Hoffmann 1977) and *S. cinereus* at elevations from 2164 to 3231 m in the Rocky Mountains of southern Wyoming. Clearly, the upper elevational limit for these shrews exceeds 1800 m, but they are much less common above this elevation.

The northern water shrew (*Sorex palustris*) is a unique shrew which, because of its semi-aquatic nature, is found only near mountain streams, ponds, or in boggy areas (Brown 1967a; Spencer and Pettus 1966; Conaway 1952; Jackson 1928). Though usually associated with running water, this species has been captured near ephemeral streams in Pattie Canyon, Missoula, County, during the dry season (Kinsella 1967). In 1952, C. H. Conaway published the "Life History of the Water Shrew" based on 119 specimens collected near Missoula, MT. He found that 49 percent of 87 stomachs examined contained aquatic insects, and that the most productive habitats were overhanging banks along cold, rapid mountain streams.

The pygmy shrew is predominantly a boreal species but is present in the western United States in two disjunct populations (Hoffmann and Pattie 1968). One encompasses eastern Washington, northern Idaho, and western Montana and the other encompasses southeastern Wyoming and northcentral Colorado. However, both of these "populations" are described by incidents of usually one to a few captures sporadically located within the given range that may represent relict populations from the late Pleistocene (see Foresman in review).

Little is known about the habitat preferences or life history of the pygmy shrew. Brown (1967a) collected six pygmy shrews from *Sphagnum* mats along the periphery of a spruce-fir bog at 9,620 feet in southcentral Wyoming. Spencer and Pettus (1966) also reported taking this species along the edges of a spruce-fir bog in Colorado. In Wisconsin and Canada, where the pygmy shrew is not a disjunct species, it occurs in, though is not restricted to, boggy habitats (Buckner 1966; Jackson 1961).

In Montana, pygmy shrews have been reported from a wide variety of habitats, and it is unclear if any specific habitat preference exists for the species there. Conaway (personal communication in Brown 1967a), using trapping data from northwest Montana, described this species' habitat as "dry areas of clearcut forest having dense ground cover." In Glacier National Park, Key (1979) collected one pygmy shrew from the floodplain on the North Fork of the Flathead River. Koford (1938) captured an individual in an open ponderosa pine stand 100 feet from the Thompson River, northwest Montana. Hoffmann et al. (1969a) report that 14 pygmy shrews have been collected from the grand-fir habitat type at the University of Montana Biological Station, Yellow Bay. Numerous individuals have been captured in the Swan Valley, western Montana (K. R. Foresman pers. comm.). Foresman (1986) collected two specimens from the South Fork of Spruce Creek, Idaho County, Idaho, in stands dominated by subalpine fir (*Abies lasiocarpa*), grand fir (*Abies grandis*) and Engelmann spruce (*Picea engelmannii*). Since this site is near the BNF, where similar habitat is abundant, it is reasonable to presume that this species occurs on the BNF.

Preble's shrew is unusual in that it is associated with dry shrub-step habitats (Hoffmann et al. 1969a). This species is represented in Ravalli County by one specimen collected in 1910, eight miles northeast of Stevensville, MT (Hoffmann and Fisher 1978). No habitat description is given, but based on adjacent undeveloped habitat, the site was probably dominated by big sage (*Artemisia tridentata*) and bunchgrasses (*Festuca* spp. and *Agropyron spicatum*) (personal observation). This species is associated with dry sagebrush habitats in Montana as seen by six specimens taken near Butte, MT, and one specimen each taken from St. Mary's, Glacier County, MT, and the Lamar Ranger Station, Yellowstone National Park, WY (Hoffmann et al. 1969a). Pitfall trapping in sagebrush habitats along the foot hills of the Saphire Range may well produce more specimens of Preble's shrew in the Bitterroot Valley.

Bats

The inactivity of bats during the day and their great mobility make it difficult to determine habitat preferences for these particularly secretive small mammals. For these reasons, less information is available for this group than others. Ten species of bats are confirmed as present in the Bitterroot Valley. Most of these probably occur to some extent on the BNF (Table 1). An additional three species are included as possibly present based on habitat affiliations and distributions.

The little brown myotis (*Myotis lucifugus*), or little brown bat, is the most common bat in Montana. It lives in summer colonies that can be found in buildings and caves throughout Montana. Other less common species of myotis such as the yuma (*M. yumanensis*), California (*M. californicus*), and long-legged myotis (*M. volans*) often occur in conjunction with colonies of little brown bats. Little brown bats may migrate south to overwinter (Hoffmann and Pattie 1968), but at least some remain (Nagorsen et al. 1993). In Alberta, 75 percent of 269 maternity colonies of little brown bats were found in buildings (Schowalter et al. 1979). This bat forages low over water surfaces during the brief period after sunset when its chironomid food is most abundant (Barclay 1991).

The yuma myotis is the second most common bat in Montana and the Bitterroot Valley (Hoffmann and Pattie 1968). This species is commonly found in colonies with the little brown bat (Hoffmann et al. 1969b). Brigham (1992) determined that the yuma bat forages predominantly in open areas and feeds opportunistically on aquatic insects, taking whatever species are abundantly available. This species likely migrates south in the fall.

The long-eared myotis (*Myotis evotis*) is widespread but uncommon as it generally occurs singly or in small numbers. In the Bitterroot Valley, it has been collected at Stevensville, Victor, Corvallis, Hamilton, West Fork Ranger Station, and Sleeping Child (Hoffmann et al. 1969b). This species is thought to be associated with coniferous forests (Hoffmann and Pattie 1968). The long-eared myotis is described by Barclay (1991) as a moth-eating bat that forages primarily within forests and on forest paths on the front range of the Rocky Mountains, Alberta. Foresman and Pearson (unpublished data) collected an individual feeding over a small pond in an Engelmann spruce bog in the Flathead Valley. The foraging conditions and behavior at this site were similar to those described by Barclay (1991) in Alberta. Roemer (1994) captured 16 individuals predominantly in moist forested habitats in northwest Montana.

The fringed myotis is rare, occurring near the northern extent of its range in Montana (Hoffmann and Pattie 1968). The first fringed myotis in the state was taken at Woodside, Montana, in the Bitterroot Valley (Hoffmann et al. 1969b). Few additional records have been added, but adult females and juveniles have been among them, suggesting that some breeding occurs within the state.

The California myotis (*Myotis californicus*) is also somewhat rare, occurring at the eastern edge and near the northern edge of its range in western Montana (Hoffmann and Pattie 1968). This species was first reported in the state from the Bitterroot where one was collected from a house in Hamilton (Hoffmann et al. 1969b). Until recently, all but one specimen had been taken from Ravalli County. Roemer (1994) captured 19 California myotis while surveying for bats on the Kootenai and Lolo National Forests, and Foresman and Pearson (unpublished data) collected one near a small pond in a spruce bog in the Flathead Valley. This species probably migrates south as do other myotis, but a number of winter records are described for British Columbia (Nagorsen et al. 1993).

The eastern small-footed myotis has been collected only at a few locations in the southern portion of the state. Many of the known collections are from the Bitterroot Valley: Stevensville, Victor, Corvallis, Woodside, Hamilton, Grantsdale, and Sleeping Child (Hoffmann et al. 1969b). The eastern small-footed myotis is thought to migrate to southern climes to overwinter (Hoffmann and Pattie 1968).

The western small footed myotis (*M. ciliolabrum*) has not been reported in the Bitterroot Valley, but eight individuals were captured by Roemer (1994) while surveying the Kootenai and Lolo National Forests, and this species may occur on the BNF. This species is not included in Hoffmann and Pattie's (1968) key to Montana mammals and was not reported during intensive surveys in the Bitterroot Valley (Hoffmann et al. 1969b).

The big brown bat maintains a wide distribution in the United States but is less common in Montana than elsewhere (Hoffmann and Pattie 1968). It occurs in a variety of habitats and is known to roost in caves and buildings. Brigham (1991) identified eight maternity colonies in hollows of large-diameter (ca. 2-m circumference) ponderosa pine snags in southcentral British Columbia. This species will also use human-made structures (Brigham and Fenton 1986) and will establish maternity colonies in buildings (Kunz 1982).

Hoffmann and Pattie (1968) suggest that most big brown bats leave the state during the winter, but evidence from British Columbia indicates that at least some individuals overwinter in caves, mines, and buildings in Canada (Nagorsen et al. 1993).

Townsend's big-eared bat ranges across Montana but is uncommon and localized within the state. Only a few maternal colonies and hibernacula have been identified in Montana. One maternal colony near the National Bison Range is set in a mine adit bordering an open ponderosa pine community (K. R. Foresman, pers. comm.). The habitat is similar to ponderosa pine stands found in lower elevations throughout the Bitterroot Valley. This species has been collected from several locations within the Bitterroot Valley including the Curlew Mine near the mouth of Big Creek, Hamilton, and Lake Como (Hoffmann et al. 1969b). Townsend's big-eared bat hibernates in caves in Montana and British Columbia (Nagorsen et al. 1993; Hoffmann and Pattie 1968).

The largest Montana bat is the hoary bat (*Lasiurus cinereus*) (Hoffmann and Pattie 1968). Because this species roosts individually in trees, it is difficult to locate and has been captured uncommonly in the state. Roemer (1994) captured only one hoary bat in 42 nights of mist netting in northwestern Montana. No record of hoary bats from the Bitterroot Valley was uncovered, but it very likely occurs on the BNF. The hoary bat migrates to more southern latitudes to overwinter (Perkins and Cross 1988; Findley and Jones 1964). Perkins and Cross (1988) found hoary bats significantly more abundant in Douglas-fir stands >200 years old. They suggested that structural diversity of older trees provided roosting habitat necessary for this species.

The silver-haired bat (*Lasionycteris noctivagans*) roosts in trees and snags and is thought to be associated with mature and old-growth coniferous forests (Campbell 1993; Hoffmann and Pattie 1968). In Oregon, the silver-haired bat selects Douglas-fir stands >100 years old but does not select ponderosa pine of the same age class (Perkins and Cross 1988). Ponderosa pine may not provide the appropriate roost sites for this species, or the habitat may be too dry. Silver-haired bats probably forage within openings in mature forests. Nine individuals were captured by Roemer (1994), primarily in moist forests in northwest Montana. Evidence from British Columbia indicates some overwintering of silver-haired bats occurs in trees and beneath the bark of older trees. A small colony has resided in a building in West Glacier at least since 1990 (pers. obs.).

The spotted bat (*Euderma maculatum*) is rare within its range across the western United States and parts of Canada (Watkins 1977; Hoffmann and Pattie 1968). This species is known from only two sites in Montana, Billings, and the Prior Mountains (Worthington 1991; Hoffmann and Pattie 1968). However, based on its current distribution and its use of open ponderosa pine habitat in British Columbia (Leonard and Fenton 1983; Woodsworth et al. 1981), this species could occur in ponderosa pine communities at the southern end of the Bitterroot Valley. In British Columbia, the spotted bat is extremely faithful to roosts in rock crevices (Wai-Ping and Fenton 1989), a habitat component also prevalent on the BNF. In general, spotted bats exist in arid habitats across the western United States (Watkins 1977). This species consumes moths and tends to fly about 10 m above the ground (Navo et al. 1992; Woodsworth et al. 1981). It may trapline and seems to be territorial (Woodsworth et al. 1981). Spotted bats are believed to migrate south to overwinter (Genter 1989).

Feeding and Habitat—Many species of bats forage over ponds, rivers, and streams where insects are abundant. Some forest species feed in natural openings and over roads and trails (Roemer 1994; Barclay 1991). Foraging height varies as does size, species of prey, and foraging time. These factors may be important in separating potential competitors. Fenton et al. (1983) found hoary bats almost exclusively associated with lights in British Columbia. In Ontario, the big brown bat was similarly drawn to lights both in towns and in urban areas (Furlonger et al. 1987). It may be that lights, which draw in noctuid moths, provide ideal foraging conditions for the energy requirements of these large bats. Other myotis were also encountered near lights, but they were found away from lights as well. Small pools in western red-cedar stands were busy drinking areas for bats in British Columbia, whereas pools with high vegetation around the edges were not used, suggesting that an open flight path for access is important (Furlonger et al. 1987). Calm water may be preferable to turbulent streams for drinking because it is less hazardous.

It is difficult to identify specific habitat relationships for bats beyond their requirements for hibernacula and day roosts and their rather general use of foraging areas with high concentrations of insects and sufficiently open flight paths for hunting. Many species seem to optimize foraging from a central roost site. Under this scenario, the best habitats are those that provide day roosts or hibernacula within close proximity to water or other concentrations of food (Brigham 1991; Furlonger et al. 1987; Barclay 1991). Furlonger et al. (1987) found "no unique associations between different species of foraging bats and specific habitats." However, radiotelemetry studies are now providing more detailed information on habitat use by bats.

Pika

The pika is a small, unusual member of the Lagomorpha. This herbivorous animal resides almost exclusively in talus slopes (Wiseley 1973). In lieu of storing brown fat for hibernation, the pika dries and caches herbaceous vegetation in "hay piles" beneath boulders to carry it through the winter months (Millar and Zwickel 1972). To protect this energetic investment, pikas are extremely territorial (Barash 1973b). Because they are also central place foragers, further intraspecific competition occurs for sites near the edges of talus slopes that provide optimal foraging areas (Kawamichi 1976). Numerous researchers (Southwick et al. 1986; Krear 1965; Kilham 1958) argue that this intense territoriality explains the lack of fluctuations observed within pika populations.

Pikas are herbivorous and so must feed in vegetation bordering talus slopes (Elliot 1980). When foraging, they remain near the protective cover of the rocks and usually stay within 5 or 10 m of the border (Tyser 1980, 1978; Barash 1973a). As a result, pikas can heavily impact abundance and composition of herbaceous plants near talus slopes (Huntly 1987; Huntly et al. 1986). An examination of 11 hay piles in a pika colony in central Idaho revealed that, although 26 plant species were present, three species (*Smilacina stellata, Apocynum androsaemilifolium, Fragaria virginiana*) made up 88 percent of the total dry weight of the hay piles (Elliot 1980).

Not all talus slopes provide optimal pika habitat. Pikas favor conditions where rocks are 10 to 12 inches in diameter (Roper 1956). Roper (1956) suggests that rocks of this size class provide ideal conditions for mazes that allow movement beneath the cover of rocks. Larger rocks may not provide sufficient protection from predation, and small ones would not allow enough space for passages beneath. Stability and aspect are also thought to be important habitat components. Steep slopes tend to be too unstable and shaded slopes may not remain snow-free long enough during the growing season (Roper 1956). Tyser (1980) found that pikas near Logan Pass, Glacier National Park, were also selective in the types of rock promontories used for surveillance activities, preferring medium-sized boulders from 0.20 to 0.99 m diameter.

Snowshoe Hare

The snowshoe hare is the common "rabbit" of western Montana forests. It is an extremely important prey species for forest carnivores such as fishers (*Martes americana*) and lynx (*Lynx lynx*), which consume primarily snowshoe hares (Powell and Zielinski 1994; Koehler and Aubry 1994; Roy 1991; Koehler 1990; Koehler et al. 1979). They also support many other carnivores, though less exclusively (see Ruggiero et al. 1994; Keith and Cary 1991; Adams 1959). Snowshoes reach their greatest numbers in mature lodgepole pine stands [25 years old (Koehler 1990) but may inhabit late seral forest as well (Powell 1991, unpublished, as cited in Powell and Zielinski 1994). Optimal habitat for snowshoe hares is consistently described as dense cover from 1.0 to 2.5 m above the ground (Wolfe et al. 1982) in the form of shrubs or dense stands of young trees (Fuller and Heisey 1986; Litvaitis et al. 1985; Wolfe et al. 1982; Adams 1959).

In western Montana and Washington, conifers are important foods for snowshoe hares (Koehler 1990; Adams 1959). This is problematic as hare populations at peak densities can become forest pests in some lodgepole pine forests (Sullivan and Moses 1986). However, hares at this latitude do not exhibit the radical 10-year cycles observed farther north where vegetation sustains heavy damage from snowshoe hare foraging in peak years (Wolff 1980). Wolff (1980) hypothesized that dampened amplitudes in hare cycles at this latitude result from a greater diversity of generalist predators and alternative prey. These predators, through prey switching, may more effectively control populations by culling hares from suboptimal habitats. A recent review of the ecology of snowshoe hares in southern montane forests can be found in Murray (in prep.).

Chipmunks

Two species of chipmunks occur on the BNF: the red-tailed chipmunk (*Tamias ruficaudus*) and the yellow-pine chipmunk (*Tamias amoenus*). The red-tailed chipmunk is most commonly associated with gaps and small openings in moist forests where shrubs occur (Foresman in review). The yellow-pine chipmunk inhabits ponderosa pine and drier, more open Douglas-fir forests. Beg (1969) found that red-tailed chipmunks dominated stands within the subalpine zone in westcentral Montana, while the yellow-pine chipmunk primarily inhabited ponderosa pine forests was present within the Douglas-fir zone where it was restricted to dry aspects where ponderosa pine dominated the canopy. In mid-slope locations where habitats integrated, the species were restricted to their respective habitats and only overlapped where sharp ecotones occurred.

Both species are associated with shrubs, which they actively climb to obtain fruits and seeds. The yellow-pine chipmunk tends to do well in early seral habitats, especially after shrubs have become established (Medin and Booth 1989; Medin 1986; Walters 1991). In westcentral Montana, Ruggiero and Pearson (unpublished data) found that the two species were sympatric in three of five moist seral ponderosa pine stands where Douglas-fir encroachment was high, and they found only yellow-pine chipmunks in two stands with low levels of Douglas-fir that had a recent history of prescribed fire. For the red-tailed chipmunk, there is conflicting data regarding its use of early seral stages. This point is discussed in detail later (see section on Disturbance). Elevationally, the two species are separated by the ranges of their corresponding habitats, though overlap does occur. The red-tailed chipmunk does well in higher-elevation, closed canopy forests, whereas the dry savanna-like habitat of yellow-pine chipmunk is most common at lower elevations.

Ground Squirrels

The columbian ground squirrel (*Spermophilus columbianus*), common in grasslands, pastures, and agricultural lands in western Montana, occurs within a limited range in the northwestern United States and western British Columbia (Hoffmann et al. 1969a). In addition to the more familiar, dry, low-elevation habitats, columbian ground squirrels inhabit moist high-elevation subalpine and alpine meadows (Hoffmann and Pattie 1968; Manville 1959). This species is also commonly found in talus slopes at higher elevations where it is sympatric with marmots (*Marmota* spp.) and pikas (for example, Tyser 1980, 1978). Though the columbian ground squirrel can inhabit more open forests, it is not present in closed canopy forests associated with mid- to late-seral stands.

Columbian ground squirrels develop extensive burrow systems. Through these earth moving activities, they provide a service to annuals and forbs which favor the disturbed patches. They also affect soil characteristics through aeration and nutrification by means of earth moving processes and the introduction of feces to these sites. Digging and burrowing activities may further alter plant communities by facilitating the invasion of non-native weeds that readily colonize such disturbed sites.

In agricultural areas and pasture lands, this species is commonly referred to by locals as a "gopher" and considered an agricultural pest. To control it, poisoning programs have been implemented. A study in the Blackfoot Valley indicated that 1080-laced bait was ineffective in controlling columbian ground squirrel populations (Malloy 1981). Although populations initially declined to zero, they returned to 20 percent of the original population size by the following year. A number of non-target species were also killed by baiting, including most small mammals on site and scavengers that consumed poisoned carcasses. Ecologically, such practices do more harm than good.

The golden-mantled ground squirrel (*Spermophilus lateralis*) is often erroneously described as a giant chipmunk by budding naturalists and visitors to national parks, but its similarity to the chipmunks extends beyond superficial morphological likeness to food habits and, to some extent, habitat. This species tends to be more omnivorous in its diet than the columbian ground squirrel, taking seeds, flowers, and fungi (Foresman in review). Like chipmunks, it favors brushy habitats and rocky outcrops. The golden-mantled ground squirrel also differs from the columbian ground squirrel in that it is asocial (Ferron 1985). It has a wider distribution in the western United States than does the columbian ground squirrel and inhabits a wider range of habitats including open areas within dry seral forests (ponderosa pine, lodgepole pine, Douglas-fir), moist high elevation stands (spruce and subalpine fir), disturbed sites, clearcuts, and alpine rock slopes (Foresman in review). This species can persist on mountain tops in patches of alpine habitat (pers. obs.).

Trapping in old-growth ponderosa pine stands in westcentral Montana and on the BNF indicates that this species is an important member of the ponderosa pine small mammal community (Ruggiero and Pearson unpublished data). Golden-mantled ground squirrels were captured in association with rocky outcrops in five of five ponderosa pine stands where they were the second most abundant species after the deer mouse.

Red Squirrel

The red squirrel seems to be restricted in habitat only by its arboreal nature and preference for conifer seeds. In the Northern Rocky Mountains, this species occurs wherever coniferous forests exist. It ranges from lower treeline in ponderosa pine communities to near upper treeline in subalpine fir forests (Foresman in review).

The red squirrel is omnivorous (Foresman in review) and will prey upon birds and small mammals (Callahan 1993). However, the red squirrel is a highly skilled pine-cone farmer that spends most of its time harvesting cone crops from the tops of conifers and caching cones for winter (Brink and Dean 1966). Its dependence on cone crops is apparent in its demographic response to years of high and low cone productivity. Halvorson and Engeman (1983) demonstrated that red squirrels born during years of high seed production on Cedar Island, Flathead Lake, had a significantly higher probability of surviving the first year than squirrels born at other times. These squirrels also lived an average of five months longer the second year, though the difference was not significant.

One result of hoarding behavior is often territoriality. The red squirrel maintains several middens where it feeds, removes seeds from cones, and caches seeds for later use. These sites are aggressively defended against conspecifics and are easily identified by great mounds of pine cone debris. Middens may be built up over many years by a single individual (which can live seven years; Halvorson and Engeman 1983). Later generations add further to such structures as territories change owners (Hatt 1943). Because of this strong dependence on cone crops and aggressive territoriality, red squirrels are probably subject to source/sink dynamics. Red squirrel populations found in post-harvest treatments may be sinks.

Middens are ecologically important sites not only for the red squirrel, but also for the American marten which uses squirrel middens as resting sites, denning sites, and access points for entering the subnivian zone in winter (Ruggiero et al. in prep.; Ruggiero et al. 1998; Sherburne and Bissonette 1993; Buskirk 1984). Middens may also function as supplemental feeding sites for deer mice and southern red-backed voles, which may visit these sites to pilfer seeds from caches or simply clean up scraps left by squirrels. Because deer mice are nocturnal and red squirrels are diurnal (see Foresman and Pearson 1995 for data on red squirrel activity patterns), deer mice would have free reign to pilfer caches at night. If such pilfering does occur, marten could take advantage of middens as baiting stations for small rodents.

Northern Flying Squirrel

The northern flying squirrel was identified by the Scientific Assessment Team as an old-growth associated species that requires old-growth components in the Pacific Northwest (Thomas et al. 1993). This species is a cavity nester that primarily nests in natural openings and woodpecker holes (Wells-Gosling and Heaney 1984; Cowan 1936). Although it has also been observed using external dray-type nests (Rust 1946; Cowan 1936), Cowan (1936) believed such nests were mostly used in summer. Because of its cavity nesting habit, the northern flying squirrel requires snags of sufficient diameter to provide for nesting habitat. This species is also primarily a fungivore, satisfying most of its dietary needs by consuming hypogeous mycorrhizal fungi (see Mycophagy) that are most abundant in mature and old-growth forests (Amaranthus et al. 1994; Clarkson and Mills 1994).

However, northern flying squirrels can exist in a variety of forest types provided that these habitat requirements are met. They have been trapped in ponderosa pine, lodgepole pine, Douglas-fir, and mixed conifer forests in the northwestern United States (Maser et al. 1985; McKeever 1960; Cowan 1936). Andersen et al. (1980) found northern flying squirrels in several forest types but recorded the highest densities in spruce-dominated forests. Witt (1992) compared populations of northern flying squirrels between old-growth and second-growth stands in the western Oregon western hemlock zone and found that northern flying squirrels were six times more abundant in old-growth forest sites. He attributed his findings to greater availability of den sites and higher productivity of hypogeous sporocarps associated with the old-growth stands. Rosenberg and Anthony (1992) also observed greater numbers of northern flying squirrels in old growth than second-growth stands in western Oregon. However, because they found higher proportions of females than males in second-growth compared to old-growth stands, and because densities were not correlated with habitat characteristics, the authors concluded that the northern flying squirrel was a habitat generalist rather than an old-growth associated species.

This species occurs on the BNF in late seral ponderosa pine and western larch-Douglas-fir stands (Ruggiero and Pearson unpublished data; Halvorson 1982), and in northwest Montana in late-seral western hemlock-western red cedar (K. A. Keating and D. E. Pearson unpublished data). For many years, a population has persisted on the University of Montana Biological Station on the east shore of Flathead Lake in association with large cottonwoods (*Populus trichocarpa*) within a late-seral grand fir stand (K. R. Foresman pers. comm.).

Northern Pocket Gopher

Two species of pocket gophers, the northern pocket gopher and the Idaho pocket gopher (*Thomomys idahoensis*), exist in the Bitterroot Valley. However, the latter is only present in an isolated population in the valley bottom (P. L. Wright, pers. comm.) and may not occur on the BNF. Foresman (in review) indicates that there is very limited data on the ecology of the Idaho pocket gopher, which has only been recognized as a distinct species for the last 20 years, but suggests that it is ecologically similar to the northern pocket gopher.

The northern pocket gopher is fossorial, inhabiting extensive underground burrows. It is therefore restricted to locations where deep soft soil is present, such as open meadows, but ranges from valley bottoms to high-elevation alpine habitats where appropriate soil conditions occur (Andersen and McMahon 1981; Tryon 1947). Pocket gophers produce mounds that are highly visible and a good indication of the species' presence. Scrivner and Smith (1981) have shown that indices of pocket gopher sign (mounds and earth plugs) can be used in place of trapping data to estimate pocket gopher density.

The digging activities of the northern pocket gopher can affect the local environment by increasing soil porosity and introducing nitrogen, phosphorous, and organic materials into the soil (see Bonar 1997 for review; Laycock and Richardson, 1975). Pocket gophers also affect community composition by favoring annuals and reducing forbs, especially dandelions (*Taraxacum officional*). On healthy rangelands, this species is thought to improve soil conditions. However, under conditions of overgrazing, pocket gophers may increase dramatically possibly due to an increase in preferred species associated with disturbance. The addition of pocket gopher disturbance then makes it difficult to restore the range even after livestock grazing has been removed (Laycock and Richardson 1975).

In northern Utah, Andersen and McMahon (1981) documented a decline in northern pocket gophers with advancing succession from alpine meadow to aspen-subalpine fir and spruce forest. They estimated northern pocket gopher densities ranged from 62 individuals/ha in alpine meadow to two individuals/ha in spruce forest. Bioenergetic analyses indicated that the climax spruce forest was food limited and that additional energy costs associated with reproduction in females may exceed the belowground available food supply within mid-seral aspen and subalpine fir. However, in northern Idaho spruce-fir forests, Scrivner and Smith (1981) found no difference between numbers of northern pocket gopher in early seral (1 to 10 yr) and late seral (80+ yr) stands, but observed significantly higher abundance in early seral (1 to 10 yr) and late seral (80+ yr) stands than in mid-seral stands (11 to 39, 40 to 79 yr).

Deer Mouse

The deer mouse is the most ubiquitous small mammal in North America due to its broad ecological tolerance. It exists in Montana at all elevations and in numerous habitats (Hoffmann and Pattie 1968; Pattie and Verbeek 1967). Some evidence suggests that deer mice avoid habitats at the wettest end of the hydrosere: bogs, fens, wet meadows, and marshes (Hayward and Hayward 1995; Clark 1975, 1971). Reichel and Beckstrom (1994, 1993) and Pearson (1991) trapped these habitats extensively in western Montana and captured very few deer mice.

The deer mouse is the paradigm habitat generalist, thriving in such a wide variety of environments that it is difficult to determine habitat affiliations. Although in forest habitats, the deer mouse seems to favor early seral stages (Walters 1991; Morrison and Anthony 1989; Ramirez and Hornocker 1981; Sullivan and Krebs 1981; Campbell and Clark 1980; Gashwiler 1970) and drier forest habitats (Foresman in review; Raphael 1988), it also inhabits mesic old-growth forest (Pearson 1994; Raphael 1988; Halvorson 1982). It has been reported to increase in abundance with increasing stand age (Pearson 1994; West 1991; Scrivner and Smith 1984), to have similar population densities between cutting treatments and uncut stands (Medin 1986), and to exhibit greater numbers in uncut versus selectively harvested stands (Medin and Booth 1989). Deer mice often associate with shrubby habitats (Belk et al. 1988) and shrubby microhabitats within forest stands (pers. obs.).

Pearson (1994) found deer mice to increase along a successional gradient in Glacier National Park. He reported that the deer mouse displayed stronger microhabitat selection than the southern red-backed vole, a habitat specialist, in four seral stages (65, 138, 256, 457 yr) of cedar-hemlock forest. He suggested that deer mice may exhibit "habitat switching" and respond to local site conditions by developing search images that manifest themselves as distinctive foraging patterns at the microhabitat scale. Such behavior would render the deer mouse a formidable competitor for resources and explain its tenacity for a wide variety of habitats.

Bushy-Tailed Woodrat

The bushy-tailed woodrat nests in rocky habitats such as caves, talus slopes, boulder fields, and cliff faces (Topping and Millar 1996; Finley 1958), but may also use snags and CWD in forest environments. Woodrats construct nests of sticks, dried vegetation, and debris used by later generations, which continue to add to their volume. Fidelity to perch sites used for feeding sites and latrines by individuals and lineages over time results in an accumulation of plant material and bones that, along with nest structures, provide storehouses of information for paleontologists (see Van Devender 1986). Middens can persist for thousands of years if they remain dry (Spaulding et al. 1983).

The social structure and finite nesting sites limit population sizes of bushy-tailed woodrats. Foraging is likely to occur in rocky areas immediately near the den, but most probably occurs in habitats bordering rocky areas (Topping and Millar 1996). The diet consists mostly of vegetation including forbs, conifer needles, fruits, seeds, and fungi (Finley 1958). Use of restricted den sites by the bushy-tailed woodrat (Moses and Miller 1992) has led to philopatry in female offspring. Woodrats exhibit strong agonistic behavior toward distantly related and unrelated individuals, while maintaining congenial relationships with closely related kin (mother-offspring).

Northern Bog Lemming

The northern bog lemming is a boreal species that occurs as a Pleistocene relict in Montana (see Foresman in review; and Pearson 1991). It was first discovered in the Camas Creek drainage of Glacier National Park

(Wright 1950). Later Weckwerth and Hawley (1962) trapped northern bog lemmings and found their remains in marten scats collected in Anaconda Creek not far from the Camas Creek location. A study of small mammals in the Rattlesnake Creek drainage produced another incidental capture in the bog-like habitat of Shoofly Meadows (Adelman 1979). Recent surveys conducted for this species have reconfirmed its presence in Shoofly Meadows (Pearson 1991) and uncovered numerous new populations of northern bog lemmings in western Montana (Reichel and Beckstrom 1994, 1993; Pearson 1991). Two bog lemmings have been captured on the BNF. One was taken in a snap trap at Meadow Creek in 1992 (Reichel and Beckstrom 1993). Another was captured in 1996 within an old-growth ponderosa pine stand in Big Creek, but this individual probably came from the adjacent old-growth mixed conifer bottom (Ruggiero and Pearson unpublished data).

Habitat of the northern bog lemming consists primarily of fens and bogs or bog-like environments that are themselves relict communities from the Pleistocene (Reichel and Beckstrom 1994, 1993; Pearson 1991; Layser and Burke 1973; Shaw 1930). However, this species has also been taken in wet meadows in Camas and Anaconda Creeks, Glacier National Park (Weckwerth and Hawley 1962; Wright 1950); old-growth hemlock (*Tsuga heterophylla*) forest, McDonald Valley, Glacier National Park (see Pearson 1991); subalpine-fir (*Abis lasiocarpa*) forest, Sunday Creek, northwest Montana (Reichel and Beckstrom 1993); and alpine habitat in Washington (Wilson et al. 1980). Reichel and Beckstrom (1994, 1993) and Pearson (1991) suggest that the presence of mat-forming *Sphagnum* spp. is a good, though not definitive, indicator for this rare lemming-mouse.

Montane Heather Vole

The heather vole is not common in western Montana but can be found in a variety of habitats (Hayward and Hayward 1995; Millar et al. 1985; Kinsella 1966; Negus 1950). In the Northern Rockies, it most often occurs within higher-elevation moist forests such as spruce-fir associations, and wet meadows, fens, and bog-like habitats (Hayward and Hayward 1995; Reichel and Beckstrom 1994, 1993; Pearson 1991; Hoffmann and Pattie 1968). Heather voles have been captured in abundance in flooded old-growth spruce-fir near the Canadian boarder along the North Fork of the Flathead River, MT (D. E. Pearson unpublished data). Reichel and Beckstrom (1994, 1993) caught 72 heather voles in fen and bog-like habitats throughout western Montana while surveying for northern bog lemmings. Although they did not survey other habitats, their success suggests that such habitats are important for heather voles.

Red-Backed Vole

The southern red-backed vole is a wide-ranging boreal species found in forested habitats throughout most of Canada and the northern United States (Hoffmann and Pattie 1968). Due to its broad distribution and community dominance in moist forests, an extensive literature has developed around this species, particularly with regard to its habitat associations (see Pearson 1994). In the central Rocky Mountains, this vole is an indicator species for the old-growth condition (USDA Forest Service 1985), and in the Pacific Northwest it is recognized by the Scientific Assessment Team as a species requiring old-growth components (Thomas et al. 1993). It is also listed as an old-growth dependent species by Lümen and Nietro (1980).

The southern red-backed vole is found in moist forests in much of the Rocky Mountains but disappears soon after stands are cut (Pearson 1994; Shepherd 1994; Raphael 1988; Medin 1986; Scrivner and Smith 1984; Halvorson 1982; Ramirez and Hornocker 1981), and young stands are thought to be habitat sinks for this species (Pearson 1994; Nordyke and Buskirk 1991).

Gunderson (1959) concluded that southern red-backed voles were associated with logs and therefore restricted to forests where logs were abundant. Other authors suggested this was also true of the congeneric California red-backed vole in the Pacific Northwest (Tevis 1956a), and Tallmon and Mills (1994) provide some evidence in support of this hypothesis. In Glacier National Park, Pearson (1994) determined that southern red-backed voles selected stands containing abundant large-diameter logs and further observed that when the distribution of these logs was heterogeneous within a stand, the voles selected those microhabitats containing large-diameter logs.

Voles (Genus *Microtus*)

Voles of the genus *Microtus* dominate grasslands, savannas, and grassy areas within forests in western Montana. These voles are herbivores, specializing in the consumption of grasses and forbs, but they also occasionally take seeds, fruits, and insects (see Foresman in review). The genus is represented by four species on the BNF: the meadow vole (*M. pennsylvanicus*), the montane vole (*M. montanus*), the long-tailed vole (*M. longicaudus*), and the water vole (*M. richardsoni*).

The meadow vole and the montane vole are often sympatric in grassland environments (Hodgson 1972; Findley 1951). Within these habitats, the two species segregate along a moisture gradient (Hodgson 1972). The meadow vole prefers moist meadows and wet, grassy areas near water and may exclude the montane vole from these habitats where the two species overlap (Koplin and Hoffmann 1968). The montane vole exhibits the greater ecological tolerance of the two (Douglas 1976; Clark 1973; Hodgson 1972; Findley 1951). Although it is most abundant in moist grassy conditions where the meadow vole is absent, it does well in dry conditions and is the more common species in dry grasslands and sagebrush (Clark 1973; Hodgson 1972). The meadow vole is absent from wet meadows in the alpine and subalpine zones, and montane voles occupy these grassy habitats in its absence (Hoffmann et al. 1969a).

It seems likely that competitive interactions play some part in the habitat segregation of these voles. When Koplin and Hoffmann (1968) removed meadow voles from wet meadows on the National Bison Range, Montana, montane voles began to move in from the drier surrounding areas. A reciprocal study conducted by Stoecker (1972) produced complementary results. Removal of montane voles from a xeric grassland resulted in the encroachment of meadow voles not previously captured there. Enclosure studies conducted by Douglas (1976) indicated that montane voles maintained larger home ranges and selected different vegetation in the presence of meadow voles. Murie (1971) concluded that the meadow vole was dominant over the montane vole in aggression experiments.

Hodgson (1972) trapped 59 sites around Bozeman, MT, to determine habitat associations of meadow and montana voles. Hodgson reported that numbers of meadow voles increased as graminoid cover ($r = 0.79$) and soil moisture ($r = 0.77$) increased. While the montane vole was weakly correlated with increased graminoid cover ($r = 0.27$), it exhibited a strong negative correlation with soil moisture ($r = 0.94$). He determined that montane voles were associated with drier habitats dominated by *Festuca idahoensis* and *Bromus inermis*. Rickard similarly (1960) found montane voles in association with habitats dominated by *Festuca idahoensis* in eastern Washington and northern Idaho. Hodgson (1972) reported both species were rare on plots where shrubs provided significant canopy cover (Hodgson 1972) except when the shrub was big sage which favored montane voles.

The long-tailed vole is generally less abundant than the other grassland voles (Clark 1973; Hoffmann and Pattie 1968) but has been captured in a great variety of habitats ranging from moist riparian areas, spruce-fir forests, and sub-alpine meadows to dry sagebrush (see Foresman in review; Clark 1973). Clark (1973) described the habitat of long-tailed voles as wetter and more structurally complex than that of other sympatric microtines. Halvorson (1982) captured long-tailed voles on recently burned Douglas-fir-western larch clearcuts in or near moist pockets of heavy cover in western Montana. He did not find this species in a similar burn on the drier south face nor did he find it on old-growth control plots on either aspect. He concluded that this vole requires moist sites with heavy cover and avoids old-growth stands. Long-tailed voles have been captured in grass-forb microhabitats within old-growth western red-cedar-western hemlock stands in Glacier National Park (pers. obs.) and often occur in forests where these microhabitat exist, such as along riparian corridors. In Pattie Canyon near Missoula, MT, Kinsella (1966) commonly trapped long-tailed voles along streams in forested habitat, and in 1964 he captured long-tailed voles in greater numbers than southern red-backed voles in the Douglas-fir-ponderosa pine forest. Clearly, this vole includes forests among its range of acceptable habitats.

The water vole is the most specialized of the voles. This vole has abnormally extended incisors and is the largest vole in the state. Its range is limited to the Northern Rocky Mountains and the Cascade Range. The water vole is a habitat specialist restricted to grass, sedge, and shrubby habitats associated with riparian areas in the alpine and subalpine zones (Foresman in review; Hoffmann and Pattie 1968).

In western Oregon, Doyle (1987) trapped water voles in mature and old-growth forests, but captures were always along the riparian area. Findley (1951) captured water voles in dry alpine meadows in Wyoming but indicated that they were most abundant near running water. In southern Alberta, Anderson et al. (1976) describe water vole habitat as mossy seeps and cold running streams and suggest that saturated soils and cool temperatures are important habitat features. Hoffmann et al. (1969a) reported collecting water voles from Bass Creek, ½ mile below Bass Lake in the Bitterroot Mountains, but did not specifically identify the habitat. Water voles have also been captured in lower Big Creek (D. E. Pearson, unpub. data) and in Sweathouse Creek drainages (Landres et al. 1994) on the BNF and probably occur in many drainages in the Bitterroot Range. Water voles occupy lush herbaceous vegetation near streams and wet alpine meadows in Glacier National Park (pers. obs.). Pattie (1967) captured water voles next to water in the alpine zone on the Beartooth plateau.

Western Jumping Mouse

The western jumping mouse prefers grassy areas, especially near water (Belk et al. 1988; Cranford 1983; Clark 1971; Negus and Findley 1959). However, this species has been captured in a variety of habitats and appears unrestricted elevationally (Hayward and Hayward 1995; Hoffmann and Pattie 1968; Brown 1967b). Negus and Findley (1959) found western jumping mice in meadows and willow-alder thickets along a stream but reported they were most abundant in aspen stands. Raphael (1988) reported that jumping mice were most abundant in spruce-subalpine fir and mature lodgepole pine stands. Pearson (unpub. data) captured this species in mature and old-growth cedar-hemlock and spruce-subalpine fir forests as well as in stream-side grassy meadows in western Montana.

Response of Small Mammals to Disturbance

Introduction

Many species of forest dwelling small mammals are poorly adapted to the dramatic habitat changes associated with stand replacing fires. Even a relatively small fire can encompass an entire local population of small mammals, thereby forcing survivors to disperse or perish on site. Thus, stand replacing fires restructure small mammal communities. Clearcutting and other associated timber harvest treatments similarly affect small mammals.

Numerous studies have addressed the effects of clearcutting and stand-replacing fire as major disturbance forces (Landres et al. 1995; Spildie 1994; Walters 1991; Ramirez and Hornocker 1981; Campbell and Clark 1980; Halvorson 1982; Stout et al. 1971), but fewer studies have targeted more moderate timber harvest practices (Shepherd 1994; Foresman and Henderson 1991; Medin and Booth 1989; Medin 1986), and only one was found that specifically addressed the effects of low-intensity underburning in ponderosa pine communities (Bock and Bock 1983). The lack of studies addressing the effects of less intensive natural fires can probably be attributed, in part, to the effective suppression of such fires in forest communities for the last century (Arno 1976).

Most studies conducted within the Northern Rocky Mountains are natural experiments or natural experiments involving treatment, and few include replication in their designs (Table 3). Shepherd (1994) used four replicate plots for each of three treatments, Pearson (1994) had three replicates for each of four stand ages, and Foresman and Henderson (1991) included four replicates in their study design. Halvorson (1982) did not replicate, but his study provides a unique design that presents both north and south aspect, paired treatments, and controls on the same ridge. Halvorson (1982) also follows four post treatment years, though he presents no pre-treatment data. Although this timeframe covers only a single microtine population cycle, few disturbance studies are this long-term. Designs used by Medin (1986) and Medin and Booth (1989) included control plots with pre-treatment and post-treatment data, as did Shepherd (1994). The Medin studies both contained two years of pre-treatment and three years of post-treatment data, while the Shepherd study captured one year of pre-treatment and presented only the first year of post treatment data from an ongoing project.

In reviewing this literature, I lean most heavily on results presented by Shepherd (1994), Pearson (1994), Foresman and Henderson (1991), Medin and Booth (1989), and Medin (1986) due to their proximity to the BNF and use of replication in their study designs.

Table 3—Primary small-mammal disturbance papers reviewed. Locations of studies, treatments examined, and major habitat types are indexed by author to provide a reference to local disturbance studies reviewed in this document.

Author(s)	Loc.	Treatment	Major habitat
Landres et al. 1994	MT	Clearcut/fire	Douglas-fir(?)
Pearson 1994	MT	Sere	western hemlock-western redcedar
Shepherd 1994	MT	Partial cut	Douglas-fir
Foresman and Henderson 1991	MT	Partial cut	Douglas-fir-western larch
Halvorson 1982	MT	Clearcut/burn	Douglas-fir-western larch
Ramirez and Hornocker 1981	MT	Clearcut	subalpine fir
Medin and Booth 1989	ID	Partial cut	ponderosa pine-Douglas-fir
Medin 1986	ID	Partial cut	ponderosa pine-Douglas-fir
Scrivner and Smith 1984	ID	Sere	Engelmann spruce-subalpine fir
Scrivner and Smith 1981	ID	Sere	Engelmann spruce-subalpine fir
Stout et al. 1971	ID	Fire	western redcedar through subalpine fir
Nordyke and Buskirk 1991	WY	Sere	lodgepole pine through subalpine fir
Campbell and Clark 1980	WY	Clearcut/part.cut	Engelmann spruce-subalpine fir
Spildie 1994	WY	Fire	Engelmann spruce-subalpine fir
Walters 1991	BC	Clearcut/burn	pacific silver fir (*Abies amabilis*)-hemlock (*Tsuga heterophylla*, *T. mertensiana*)

Three studies, Landres et al. (1994), Foresman and Henderson (1991), and Halvorson (1982), were conducted within or near the BNF and represent the moist, seral ponderosa pine and Douglas-fir communities of primary interest in this review. Among these studies, moderate and extreme harvest treatments and fire are addressed.

Review of Disturbance and Succession Literature

Small mammal communities of western Montana can vary in richness and complexity from simple systems of one or two species to complex associations with representatives from several ecological guilds. Many small mammal communities of western Montana are dominated by one or two species, while other species add more to the richness of an assemblage than to numbers and biomass (pers. obs.). As a result, the body of literature generated by studies of small mammal responses to disturbance focuses primarily on only a handful of species: southern red-backed voles, deer mice, yellow-pine chipmunks, red-tailed chipmunks, and generally one of three species of *Microtus*. These species are the most common small mammals associated with late successional forests and post-disturbance conditions. Other species have received variable attention depending on their local abundance at study sites.

Shrews—Shrews are seldom addressed in disturbance literature because of their poor representation in many trapping studies. Generally, only cinereus and vagrant shrews are reported on. Their response to disturbance is not clear from the information currently available. This is partly due to their low capture rates in many trapping data sets.

Spencer and Pettus (1966) captured vagrant and cinereus shrews in both clearcut and uncut subalpine fir forests in Colorado. They determined that the vagrant shrew was more common in the clearcut than the cinereus shrew, but that both species selected the moist forest and wet, marshy habitat over the clearcut. In British Columbia, Walters (1991) captured shrews in burned and unburned clearcuts, but most were caught in adjacent old-growth coniferous forest. When trapping a burned stand, a 22-year-old clearcut, and uncut mature forest stand, Landres et al. (1994) captured shrews only in the uncut stand. However, the uncut stand was probably influenced by the presence of open water absent from other sites.

Ramirez and Hornocker (1981) caught cinereus shrews in both cut and uncut stands. In some stands, shrews were more abundant in the forest while in others, they were more abundant in clearcuts. The vagrant shrew was absent from clearcut subalpine fir-*Luzula hitchcockii* habitat while abundant in forested stands of this habitat type. In the subalpine fir-clintonia (*Clintonia uniflora*) habitat type, the vagrant shrew was more abundant in clearcuts. Medin and Booth (1989) found that shrews significantly declined after low-intensity, single-tree selection logging of Douglas-fir. However, in similar habitat, more intensive diameter-cut logging had no apparent affect on shrews (Medin 1986). Seventy-seven percent of the shrews captured on a burn chronosequence in Grand Teton National Park were found in forest controls (Spildie 1994). Hayward and Hayward (1995) found that vagrant and cinereus shrews increased with increased forest complexity, number of canopy layers, and stand age. The authors did not separate the two shrews for their habitat use analysis.

It seems that shrews are more affected by a moisture gradient than a successional gradient (see Habitat Associations). Shrews may select older forests, but it is unclear as to whether this selection reflects an association with wetter microhabitats found within such forests or some other feature such as the greater structural complexity these forests provide. On sites where cutting results in greatly increased temperatures and desiccation, shrews are likely to decline or disappear after treatment.

Bats—Little data exist to address responses of bats to disturbance, and none could be found for the Northern Rockies. Most data from the Pacific Northwest indicate that many species of bats require the structural diversity of roost sites associated with mature to old-growth forests, and therefore decline in response to cutting (Thomas and West 1991; Thomas 1988; Perkins and Cross 1988). Thomas (1988) and Thomas and West (1991) reported that bat activity was 2.5 to 9.8 times higher in old-growth Douglas-fir forests than in younger stands and concluded from observed activity patterns that bats were using older stands for roosting.

Perkins and Cross (1988) determined from mist net studies that hoary and silver-haired bats were more abundant in stands >100 yrs old, but that silver-haired bats selected Douglas-fir over ponderosa pine within the 100+ age class. They concluded that the structural components of the older stands may better provide roosting habitat for these tree-roosting bats and suggested that different tree species will develop quality roosting characteristics at different rates.

Chipmunks—The yellow-pine chipmunk's range broadly encompasses much of the northwestern United States, whereas the red-tailed chipmunk is limited to isolated pockets mostly within the former's range (Hoffmann and Pattie 1968). In western Montana, where the two species are sympatric, habitat segregation is observed along an altitudinal and a moisture gradient. Beg (1969) described strong habitat separation between the red-tailed and the yellow-pine chipmunk in western Montana. He consistently found the red-tailed chipmunk in more mesic, higher elevation forests than the yellow-pine chipmunk, which remained in dry ponderosa pine and Douglas-fir habitats. Based on this habitat separation, the yellow-pine chipmunk could be expected to dominate in the hotter, drier conditions of early succession.

Medin (1986) reported that yellow-pine chipmunk densities in Douglas-fir-ponderosa pine forests of Idaho doubled after diameter-cut logging and were significantly higher than on the unlogged control. Medin and Booth (1989) noted a similar response by yellow-pine chipmunks to less intensive, single-tree selection logging within the same habitat in a nearby drainage. In British Columbia, Walters (1991) observed even greater increases in abundance of yellow-pine chipmunks in response to clearcutting of a hemlock forest. In a clearcut treatment followed by no burning, chipmunks increased 2.75 times more than they did in the forested control, whereas in an adjacent clearcut treatment that was followed by burning, populations increased 3.75 times more than the forest population. These results suggest that yellow-pine chipmunks are favored by disturbance and that the more severe the disturbance, the greater the numerical response.

The red-tailed chipmunk also increases in response to cutting, but the findings are less consistent. Results presented by Ramirez and Hornocker (1981) for northwestern Montana showed numbers of red-tailed chipmunks were similar between uncut forest and 11- to 15-year-old clearcuts, while 5-year-old clearcuts contained only half as many animals as the uncut stand for the subalpine fir-*Clintonia uniflora* habitat type. However, in the subalpine fir-*Luzula hitchcockii* habitat type, chipmunks were much more abundant in clearcut than in the uncut stand where no chipmunks were caught.

Landres et al. (1994) observed an increase of approximately 50 to 66 percent in red-tailed chipmunks on a 6-year-old burn compared to an adjacent uncut stand and an uncut wilderness control. This increase apparently continues into the early pole stage as they found numbers of red-tailed chipmunks in a 26-year-old clearcut were more than double those on the same controls. An examination of Scrivner and Smith's (1984) data for spruce-fir stands in Idaho also reveals that red-tailed chipmunks were more abundant in 1- to 10-year-old stands than in 80+ year-old stands, and that they were most abundant in mid-seral communities. Foresman and Henderson (1991) reported that red-tailed chipmunks were five times more abundant on selectively cut sites than on forested controls.

Halvorson (1982) followed numbers of chipmunks for four years after clearcutting and burning of 180- to 200-year-old Douglas-fir-western larch stands in western Montana. His design included a treatment and control on the north and the south aspect of Newman Ridge. Red-tailed chipmunks on the hotter, drier south aspect exhibited extremely high numbers in the forest but did not appear on the burn until the third fall when three individuals showed up. In the fourth year numbers increased to 15 animals, but this may have been overflow from the forest population that had doubled to 34 animals over the same period in response to a mast year. The south-aspect clearcut population quickly declined to four individuals in the final year of the study. On the north aspect, the forest population exhibited lower numbers than on the south, although this population also more than doubled in response to high seed fall. The north-aspect burn produced animals sooner (the second year) than the south burn did and quickly increased to populations that exceeded those in the forest by more than two-fold in the final year. The rather different results described for the two aspects suggest that the variables differentiating the two study sites may be important in predicting the response of red-tailed chipmunks to disturbance.

Although the design employed by Halvorson does not allow a determination of causal forces, it serves to identify important variables for future study. The major differences between north and south aspect were moisture, burn intensity, and the remaining cover resulting from the differing burn intensities. The initial slow response of chipmunks to the higher intensity south burn may be due to the greater reduction of vegetation and woody structure there. Better cover left on the north burn may have provided greater security for foraging, while vegetation may have supplied cover and more abundant food in the form of berries and seeds. However, the forest controls differed as well with regard to chipmunk populations. It may be that red-tailed chipmunks, which generally occur in more mesic forests at higher elevations, find a clearcut on a south-facing slope too hot and dry, while the closed forest on the north aspect may offer insufficient shrubby habitat, with the optimal conditions lying somewhere in between (in other words, the more mesic clearcut and the drier, more open forest stand).

The only disturbance study reporting on sympatric populations of yellow-pine and red-tailed chipmunks is that of Shepherd (1994) in the Swan Valley, western Montana. Shepherd found that yellow-pine chipmunks decreased on control grids after cutting while increasing on the overstory-removal treatments. Although increases on treatments were not statistically significant, the response was consistent with outcomes observed in other studies and the chipmunks similarly appeared to respond to the treatment in proportion to the degree of cutting. The greatest increase in yellow-pine chipmunks took place where the greatest disturbance occurred. Red-tailed chipmunks, in contrast, exhibited the reciprocal response; they increased on the control grid, while decreasing on the treatments in proportion to disturbance. This unusual response of the red-tailed chipmunk in the context of the results reviewed above suggests that there may be a competitive interaction between these two species that affects the red-tailed chipmunk's reaction to disturbance. In all the allopatric studies reviewed, the red-tailed chipmunk exhibited marginal to dramatic increases in abundance in response to disturbance. The only apparent decrease was on the south slopes in Halvorson's (1982) study. Careful examination of Halvorson's and Shepherd's data might suggest an appropriate experimental design to determine the degree to which competition versus vegetation and topographic variables may affect the response of the red-tailed chipmunk to disturbance.

Ground Squirrels—The columbian ground squirrel tends to increase after disturbance. Information about this species is seldom reported in small mammal-disturbance studies, but it is known to increase after cutting and after fire in response to the increase in the grasses and forbs that it feeds on. Ramirez and Hornocker (1981) reported that the columbian ground squirrel was abundant in alpine meadows adjacent to their study sites, and even more abundant in 5- to 15-year-old clearcuts. Columbian ground squirrels were at least three times more abundant in clearcuts versus forest plots that served as controls.

Golden-mantled ground squirrels were reported in only one study. Medin (1986) found that golden-mantled ground squirrels increased in response to diameter-cut logging in ponderosa pine-Douglas-fir forests in Idaho. Where present, the golden-mantled ground squirrel and columbian ground squirrel are likely to increase in response to disturbance, as their habitat needs are favored by such changes.

Red Squirrel—Red squirrels are tree squirrels, and their local and regional distributions are defined primarily by the distributions of conifers (Hoffmann and Pattie 1968). Although this species is known to consume a variety of substances (Callahan 1993), its life history is intertwined with the forest environment with which it evolved (Smith 1970). Halvorson and Engeman (1983) demonstrated red squirrel dependence on cone crops by showing that offspring survival is significantly correlated with cone production in island populations in ponderosa pine-Douglas-fir communities on Flathead Lake. They showed that high cone yields greatly increased the probability of survival. The extent to which low-intensity management, thinning, etc., and low-intensity fire affect habitat quality for this species will largely depend on its effect on cone crops and conifer diversity.

Data for red squirrels is seldom reported in disturbance literature because they tend to avoid traps traditionally used in small mammal research (pers. obs.). However, Medin and Booth (1989), Medin (1986), and Halvorson (1982) provide some information about the effects of timber harvest on this species. Halvorson (1982) reported capturing red squirrels, but only in forested controls, reinforcing the notion that red squirrels respond qualitatively to canopy removal by disappearing from recent clearcuts. Medin and Booth (1989) noted that numbers of red squirrels were high on both treatments and controls after single-tree selection logging but did not attempt to quantify their numbers. Medin (1986) observed a decline in numbers of red squirrels after more intensive diameter cut logging within the same watershed but concluded that methods employed in his study were insufficient to effectively determine quantitative changes in red squirrel populations. These results suggest that red squirrels decline in response to tree removal, and selective cutting may generate sink habitats if reduced tree densities and/or removal of dominant trees decreases cone production below some minimum threshold necessary to maintain population growth rates ≥1.

Northern Flying Squirrel—Northern flying squirrels are nocturnal and generally not captured unless they are targeted with squirrel traps. Less is known about this species than other squirrels because of its nocturnal nature. Although the northern flying squirrel is widely distributed within forested regions of the United States (Hoffmann and Pattie 1968), it is thought to be an old-growth associated species (Thomas et al. 1993) due to its requirements for nesting cavities in medium- to large-diameter snags (Cowan 1936) and its dependence on hypogeous mycorrhizal fungi (Rosentreter et al. 1997; Maser et al. 1978; Maser et al. 1985; McKeever 1960; see Mycophagy), which are most abundant in mature and old-growth forests (Amaranthus et al. 1994).

Rosenberg and Anthony (1992) compared northern flying squirrel populations between second-growth and old-growth Douglas-fir stands in Oregon and found that, although numbers were slightly higher in old-growth stands in both years, they did not differ significantly. They determined that squirrel densities were not correlated with habitat characteristics and concluded that "flying squirrels may be habitat generalists." In northern Utah, Andersen et al. (1980) observed higher densities of flying squirrels in spruce-dominated forests (1.2 to 2.5 squirrels/ha) than in earlier seral aspen-dominated (*Populus tremuloides*) stands (0.2 to 1.8 squirrels/ha), but squirrels were only slightly more abundant in spruce-dominated forests than in aspen stands (0.2 to 2.1 squirrels/ha). In western Montana, Halvorson (1982) captured northern flying squirrels on forested control plots, but not on burned clearcuts, and reported that 77 percent of his captures were on the south-facing as opposed to the more mesic north-facing 180- to 200-year-old Douglas-fir-western larch stands.

Witt (1992) trapped 165 northern flying squirrels 1,023 times over five years in old-growth and second-growth forests in western Oregon. Density estimates indicated that flying squirrels were six times more abundant in old-growth than in second-growth forests. These results were supported by a catch-per-unit effort index. Witt (1992) complemented trapping data with radiotelemetry data and found that three of five squirrels had den sites located outside their estimated home ranges. He suggested that trapping results may bias toward foraging habitat, thereby ignoring the critical denning aspect of habitat use.

In light of Witt's findings, which are supported by those of Andersen et al. (1980) and Halvorson (1982), results presented by Rosenberg and Anthony (1992) do not contradict a conclusion that northern flying squirrels are old-growth associated species. It is, rather, their conclusions that are contradictory, as the lack of selection for habitat features may have been due to trap bias (Witt 1992) or trap insensitivity to the scale of variables being measured (see discussion in Pearson 1994). Foraging in second-growth stands by squirrels living in the adjacent old growth could easily account for the results observed by Rosenberg and Anthony (1992), and the higher numbers of squirrels that they reported in old growth suggest that this may have been the case. Although in all studies reviewed northern flying squirrels consistently avoided clearcuts, their use of second-growth stands suggests that, although second-growth may not fulfill all requirements of flying squirrels, it may contribute to their resource base when occurring in conjunction with mature and old-growth forest in a habitat mosaic.

Northern Pocket Gopher—The northern pocket gopher is not generally included in studies of small mammal succession, but a few studies in the West have reported on this species. Scrivner and Smith (1981) found that northern pocket gophers were most abundant in the youngest (1 to 10 yr) and oldest (80+ yr) stands of spruce-subalpine fir forests that they studied in Idaho, although the authors found no difference in abundance between these two categories. Stands between these age classes contained similar numbers of pocket gophers when compared to each other. Andersen and McMahon (1981) determined that food was a limiting factor in later seral stages for northern pocket gophers living in forests along a spruce-subalpine fir sere in Utah. Their capture data supported their bioenergetic analysis. Densities ranged from 62 individuals/ha in the meadow to two individuals/ha in the spruce forest. In general, pocket gophers prefer soft deep soils that facilitate movement beneath the ground (see Habitat Associations).

Southern Red-Backed Vole—In the Northern Rocky Mountains, the red-backed vole (*Clethrionomys gapperi*) and the deer mouse (*Peromyscus maniculatus*) are the most commonly reported species in disturbance studies. The southern red-backed vole is considered an old-growth associated species (Thomas et al. 1993). It is typically abundant in mature to old-growth forests and reported to crash or to decrease to very low numbers after clearcutting and fire (Sullivan and Boateng 1996; Landres et al. 1994; Spildie 1994; Ramirez and Hornocker 1981; Medin 1986; Halvorson 1982, 1981; Campbell and Clark 1980). This species can be found in early seral lodgepole pine stands, but such habitat is believed to be a dispersal sink (Pearson 1994; Nordyke and Buskirk 1991). Under some less intensive harvest treatments, southern red-backed vole populations may persist after cutting, at least for a few years (Shepherd 1994; Foresman and Henderson 1991; Medin and Booth 1989; Ramirez and Hornocker 1981; Campbell and Clark 1980), but it is not known whether such sites function as sink populations.

A number of factors may prevent southern red-backed voles from expanding beyond late seral forests. Getz (1962) and Odum (1944) argued that the southern red-backed vole's inefficient use of water restricted it to moist habitats. Other authors have suggested that a dependence on hypogeous sporocarps for food restricts the congeneric California red-backed vole to mature forest where this food is present (Mills 1995; Martell 1981; Maser et al. 1978). Although the southern red-backed vole depends on fungi for food, it is a less strict mycophagist than the California red-backed vole (see Mycophagy). Harvey et al. (1976) demonstrated that decomposed woody debris in the organic layer was an important substrate for fruiting of hypogeous fungi in western Montana, so it is possible that the southern red-backed vole forages for sporocarps near decaying logs in this area. Current data on habitat associations of southern red-backed voles in the Northern Rocky Mountains indicate that large-diameter logs are important habitat components for this species (Pearson 1994; Nordyke and Buskirk 1991). The primary role of logs and other CWD is likely that of hiding and escape cover; however, sporocarp productivity in these microhabitats probably also plays a role.

Nordyke and Buskirk (1991) determined that southern red-backed voles might function as an indicator species for the old-growth condition. They found that this species increased in abundance with an increase in old-growth condition rating in a relationship that could be described using a second degree polynomial model. Scrivner and Smith (1984) also found a general correlation between southern red-backed vole abundance and stand age.

Pearson (1994) reported a strong, positive, linear correlation between abundance of southern red-backed voles and stand age, and concluded that weaker correlations seen elsewhere may be due to: 1) the incorporation of measurements of old-growth attributes >1 m high in old-growth indices; 2) the use of too few seral stages in regression analyses; or 3) inclusion of less distinct seral stages which might incorporate ecotones between plateaus along the successional gradient or include more than one sampling point within a plateau. He suggested that, within the Northern Rocky Mountains, southern red-backed voles may be an excellent indicator of old-growth conditions at or near ground level, and, if used in conjunction with other old-growth associated species from different ecological guilds, an indicator guild might be developed that would allow assessment and monitoring of old-growth quality for multiple strata within a stand.

Deer Mouse—The deer mouse is the paradigm habitat generalist, and can be found in any successional stage (Landres et al. 1994; Spildie 1994; Ramirez and Hornocker 1981; Walters 1991; Medin 1986; Scrivner and Smith 1984; Campbell and Clark 1980; Halvorson 1982; Stout et al. 1971). In general, this species has been reported to increase in response to disturbance (Landres et al. 1994; Spildie 1994; Bock and Bock 1983; Ramirez and Hornocker 1981; Walters 1991; Halvorson 1982; Stout et al. 1971), but Medin and Booth (1989) reported a decline for this species after single-tree selection logging. Pearson (1994) found that deer mice increased in abundance with increasing stand age for stands 65, 150, 350, and 450 years old, and Scrivner and Smith (1984) obtained similar results. Sullivan (1979c) concluded that a clearcut in British Columbia was a dispersal sink for deer mice. The response of this species to disturbance may depend on ecotypic variation between populations and the effects of the disturbance on local food availability.

Microtus—Three species of voles are affected by the type of disturbance defined in this review: meadow voles, long-tailed voles, and montane voles. In general, voles increase qualitatively in response to disturbance. The species that comes to dominate a site will depend on moisture, elevation, and possibly founder effect given the nature of interspecific interactions noted between montane voles and meadow voles (see Habitat Associations).

Halvorson (1982) observed long-tailed voles in abundance on the moist, north-aspect, burned clearcut, but found them to be rare on the south burn and absent on both forest controls. Long-tailed voles were also the dominant vole taken by Foresman and Henderson (1991) in partial cut treatments of Douglas-fir-ponderosa pine stands. Although they were not captured in the forest, they were moderate to abundant in the treatments. On the BNF, montane voles dominated a 26-year-old clearcut and were present on a 6-year-old burn but were absent from forest controls (Landres et al. 1994). Except for a few water voles caught near water, this was the only vole reported from this study site. Ramirez and Hornocker (1981) observed meadow voles and long-tailed voles in low to moderate numbers on some, but not all, clearcuts ranging from 5 to 11 years in northwest Montana; but they trapped none of either species within forest controls.

Community Response to Disturbance Richness and Diversity—No single small mammal disturbance study in the Northern Rocky Mountains examines changes in diversity, species composition, and/or biomass along a complete successional gradient that includes grass/forb, shrub, sapling, young forest, mature forest, and old-growth forest seral stages. Most studies compare recent clearcuts in grass/forb, shrub, or sapling stages with mature or old-growth forest and few of these studies present data for changes in abundance, diversity, or total biomass between controls and treatments.

In comparing young clearcuts (5-15 years) with uncut forest, Ramirez and Hornocker (1981) observed greater total small mammal abundance and much greater biomass in young clearcuts than in uncut forests. This was primarily due to the abundance of columbian ground squirrels in the uncut stands. However, red squirrels, which were likely common in the uncut forests, were not sampled. So these data are probably biased in this respect. Landres et al. (1994) trapped a young stand in a 26-year-old clearcut, an adjacent, uncut, wet forest, and an adjacent uncut dry forest. They captured 50 individuals representing four species in the young stand compared to 132 individuals from six species in the adjacent wet forest and 84 individuals representing four species in the adjacent dry forest. Medin and Booth (1989) showed a slight increase in biomass and species richness following single-tree selection logging (removal of about 22 trees/ha >23-cm diameter) of ponderosa pine-Douglas-fir dominated stands in Idaho. The increase in biomass was probably due to a dramatic increase in the yellow-pine chipmunk, one of the largest community members captured, in the logged stands. Cary and Johnson (1995) found that old-growth stands on the Olympic Peninsula produced 1.6 times more small mammals and 1.5 times more small mammal biomass than managed stands.

It is unclear how diversity and biomass change in response to clearcutting or moderate timber harvest within Northern Rocky Mountain forest ecosystems. Abundance may increase in the initial grass/forb and shrub stages due to increases in early seral small mammals such as *Microtus*, columbian ground squirrels, and chipmunks. This increase phase is probably followed by a rapid decline as grasses and shrubs give way to young trees and early seral small mammal species decline with the loss of their newly acquired habitat. Small mammal abundance probably does not begin to increase again until forests mature and the canopy opens up allowing the understory to develop. Diversity may follow a similar coarse reaching its peak in the old-growth condition when gap dynamics come into play providing a diversity of understory vegetation including grass/forb and shrub patches as well as greater structural complexity on the forest floor that can provide for early- and late-seral small mammal species. An important factor that should be considered when assessing diversity in relation to disturbance and succession is seasonality. Many early-seral species described here hibernate (columbian ground squirrels, golden-mantled ground squirrels, and yellow-pine chipmunks) whereas most late seral species do not. For example, the tree squirrels remain active year-round. Additionally, *Microtus* exhibit more radical population fluctuations than do red-backed voles, their late-seral ecological equivalents. Therefore, late-seral forests could be expected to maintain more constant diversity and biomass both seasonally and annually than sites that have recently been disturbed. More comprehensive research will be necessary to better understand changes in small mammal communities such as diversity, abundance, biomass, and species composition as they relate to the entire successional gradient.

Management Recommendations

Habitat requirements of small mammals are as diverse as the taxonomic groups presented in this review. Fortunately, most small mammals are resilient to natural disturbances due to their high reproductive potential, excellent dispersal capabilities, and ability to persist in relatively small patches of habitat. Some habitat specialists reviewed here are unlikely to be affected by forest management practices because of their unique habitat affiliations. For example, pikas and dwarf shrews are associated with talus slopes and rocky outcrops. Numerous other species benefit from processes that reinitiate succession and open forest canopies. These include meadow voles, long-tailed voles, golden-mantled ground squirrels, columbian ground squirrels, yellow-pine chipmunks, and others. Clearcuts, seed tree cuts, shelterwood cuts, and underburning favor these species. The deer mouse seems impervious to nearly any management practice. Although it responds with changes in abundance and demography, this species can exist in most altered habitats. Many small mammal species require no special management considerations for their survival due to unique habitat affiliations or associations with early seral stages.

However, several old-growth associated species such as northern flying squirrels, red-backed voles, and tree-roosting bats respond negatively to timber harvest, and other habitat specialists like bog lemmings and water shrews may be negatively affected by logging if bog hydrology is altered or water quality is degraded. Moreover, although mere existence of a complement of small mammal species may fulfill mandates for diversity, it may not provide the conditions necessary for maintenance of many small-mammal-driven ecological processes. For instance, the mere presence of red-backed voles does not ensure that martens and boreal owls will have a sufficient prey base to persist in an area that otherwise meets their needs, nor does it ensure that dispersal of spores of hypogeous mycorrhizal fungi will occur above some minimum threshold necessary for maintenance of fungal or host populations. Thus, I focus management guidelines and the discussion of maintaining healthy small mammal populations in forest ecosystems on the subset of species that are most affected by timber harvest.

Coarse Woody Debris

Wildlife management is in large part habitat management. Arguably, the single most important habitat feature for forest-dwelling small mammals is coarse woody debris. Whereas generalist species, such as deer mice, use CWD opportunistically for hiding cover (Barnum et al. 1992; Platz and Kirkland 1992), habitat specialists such as red-backed voles may *require* CWD for persistence. Coarse woody debris facilitates predator/prey interactions in winter by providing predators like martens and weasels access to subnivian small mammals (Sherburne and Bissonette 1994; Corn and Raphael 1992). At other times, CWD functions to mediate predator/prey interactions by providing small mammals with hiding and escape cover, thereby potentially dampening small mammal population cycles, and stabilizing small mammal and predator communities. Red squirrels often construct middens in association with CWD, possibly to take advantage of the escape cover and feeding promontories offered by these structures. In addition to their obvious importance to the squirrels, middens provide critical den sites (Ruggiero et al. 1998) and resting sites for marten (Ruggiero et al. in prep.; Buskirk 1984) and can support higher densities of red-backed voles than surrounding forest (Ruggiero and Pearson in prep.). Coarse woody debris functions more directly in nutrient cycling (Maser and Trappe 1984), as nurse logs in moist forest systems (Harmon and Franklin 1989), and possibly as fruiting sites for hypogeous mycorrhizal fungi (Waters et al. 1996; Amaranthus et al. 1994; Harvey et al. 1976). Therefore, management favoring CWD supports not only small mammal communities, but processes integral to forest ecosystems. To maintain long-term forest ecosystem integrity, ecosystem management must recognize the importance of CWD to wildlife in forest ecosystems and manage for this component accordingly.

Historical Coarse Woody Debris—In most managed forest stands, the largest-diameter CWD has been burned and removed since harvesting began, leaving us with little evidence of presettlement conditions (Harmon et al. 1986). Additionally, we have greatly reduced CWD recruitment through timber harvest. These practices have carried us to the brink of a CWD bottleneck for many stands especially in drier cover types such as ponderosa pine and dry western larch-associations. Although decadence is occurring within Douglas-fir on these sites, it is not large-diameter material and will likely be removed in the process of treatment (D. Lockman, Biologist, Bitterroot National Forest, pers. comm.). Even with careful management, CWD within such stands will not regain natural age- and size-class distributions for many years. Therefore, while CWD reductions may be in order in some cover types such as white-bark pine where white pine blister rust has resulted in high mortality of large-diameter trees, active recruitment will be necessary in many stands entering their second rotation and probably all stands entering their third rotation. However, restoring historic conditions is made difficult due to our lack of knowledge of presettlement CWD.

For drier cover types on the BNF, low-intensity fires occurring at frequent intervals (Arno 1976) would function to reduce and recycle fine fuels and smaller woody debris (_6 inch dia.). Larger debris are more resistant to low-intensity fires (Reinhardt et al. 1994, 1991; Robichaud et al. 1994), and stand-replacing fires would increase CWD due to the transfer of standing biomass to the CWD layer (see Brown and See 1981). Therefore, fire ecology in fire-dependent communities probably favors larger diameter CWD while minimizing finer woody materials and fine fuels by frequently recycling these. Larger diameter material would often be left only partially burned (see Reinhardt et al. 1994), and low intensity fires would select for larger trees (due to thicker bark and deeper roots) that would ultimately become large-diameter CWD.

Small Mammal use of Coarse Woody Debris—Developing guidelines for CWD management requires some understanding of how small mammals interact with CWD and what attributes appear to be limiting. Diameter and volume of CWD appear to be the most important factors for red-backed voles, with larger diameters and greater volumes being favored (Tallmon and Mills 1994; Pearson 1994; Nordyke and Buskirk 1991; Hayes and Cross 1987). Though stage of decay may also be important, it is unclear whether earlier stages of decay or later stages are preferred (Tallmon and Mills 1994; Pearson 1994; Nordyke and Buskirk 1991; Hayes and Cross 1987; Doyle 1987). The answer may depend on whether the structure is being used more for feeding sites or for hiding and escape cover, and the relationship may change seasonally depending on phenology of vegetative cover and fruiting of truffles.

No data exist to assess how length of logs affects use by small mammals, but fluorescent pigment tracking shows that logs are used as travel routes by southern red-backed voles (Pearson 1994), shrews (McCracken 1990), white-footed mice (*Peromyscus leucopus*) (Barnum et al. 1992; Planz and Kirkland 1992), deer mice, and long-tailed voles (D. E. Pearson unpublished data). Longer logs provide secure travel routes over greater distances within an animal's home range and may be more valuable. Pearson (1994) suggested that the spatial distribution of CWD may also affect use patterns by small mammals. He concluded that red-backed voles selected more for microhabitats having CWD when logs were patchily distributed.

Coarse Woody Debris Management Guidelines—Though many studies have concluded that CWD is an important habitat component for small mammals (Tallmon and Mills 1995; Pearson 1994; Nordyke and Buskirk 1991; Hayes and Cross 1987; Gunderson 1959), guidelines for managing CWD (logs primarily) for wildlife have been poorly developed. For instance, Harmon et al. (1986) gave the most extensive review of CWD in the United States to date, but they did not address the issue of CWD management. Hunter (1990) emphasized the importance of CWD but did not provide sufficient guidelines for its management. Carey and Johnson (1995) suggested that "15 to 20 percent cover of CWD, well distributed across a site, would be adequate for most small mammals." However, they did not adequately address the issue of recruitment of CWD.

The BNF Forest Plan currently has no provisions for management of CWD for wildlife (BNF Forest Plan 1987). It does, however, incorporate CWD guidelines proposed by Harvey et al. (1987) for management of mycorrhizal fungi in Northwest Montana. These guidelines recommend managers retain 10 to 15 tons/acre (2.2 to 3.4 kg/m^2) of CWD greater than 6 inches (15 cm) in diameter. The question then arises: If implemented, would CWD guidelines designed to manage for the needs of mycorrhizal fungi be sufficient to also fulfill the needs of small mammals? Not enough research has been conducted to answer this question definitively. Certainly small mammals would benefit from the hiding and escape cover provided by following these guidelines. Additionally, if these guidelines succeeded in maintaining healthy hypogeous fungi populations, small mammals would benefit from the food resource offered by the resulting truffles. Nonetheless, such an approach may be too simplistic to address the more complex needs of small mammals such as large-diameter logs, range of decay classes, logs elevated aboveground, etc. For example, a "boardwalk" of 15-cm diameter lodgepole stems from blowdown provides high CWD cover woody debris for truffles, but does not provide appropriate habitat. Mean diameter of CWD probably better predicts small mammal species composition and abundance than does number of CWD stems, but generic guidelines that simply assign a minimum value (Carey and Johnson 1995; Brown and See 1981; Harvey et al. 1987), even based on a mean, will not likely adequately fulfill CWD requirements for small mammals. Furthermore, recruitment of CWD must be addressed if CWD is to be maintained on a site in conjunction with timber harvest.

Brown and See (1981) defined CWD management as a trade off between its beneficial and detrimental effects. They concluded that volumes of CWD up to 15 tons/acre (3.4 kg/m^2) would not result in an excessive fire hazard, but felt that volumes in the range of 15 to 20 tons/acre (3.4 to 4.5 kg/m^2) could "diminish fire protection efficiency." They also recommended that hard logs could be removed for economic values, while soft wood (material in late decay stages) could be left to fulfill the ecological role of CWD for ectomycorrhizal activity. However, more recently Reinhardt et al. (1991) suggested that CWD volumes up to 50 tons/acre (11.2 kg/m^2) for fuels >15-cm diameter did not result in excessive fire hazards. Given the importance of logs in earlier stages of decay for wildlife (Pearson 1994; Hayes and Cross 1987) and for recruitment of CWD into later decay classes, removal of this component would deleteriously affect small mammal communities and ecological processes.

CWD management should focus on recruitment of logs of all size classes. However, past management practices have resulted in a bottleneck in recruitment of large-diameter CWD, which research to date has shown to be the most important for wildlife habitat. Therefore, large-diameter CWD should be a recruitment target until the system is brought back into balance. Large-diameter CWD at volumes <50 tons/acre (11.2 kg/m^2) should not pose undue fire risk (Reinhardt et al. 1991).

Coarse Woody Debris Guidelines for Cavity-Nesting Birds—Because logs, branches, upturned roots, and stumps come from trees, and logs often develop from snags, CWD management is integrally linked to tree and snag management. Furthermore, snags provide den sites and roosting sites for many small mammals including tree-roosting bats, red-squirrels, flying squirrels, woodrats, and chipmunks. It is therefore reasonable to examine snag management guidelines for cavity-nesting birds to determine whether CWD needs on the forest floor can be met through snag management.

Given that snags are by definition more decayed than live trees, recruiting CWD only from snags will result in a decay class distribution skewed toward more advanced decay classes. This is problematic because later decay classes lack many CWD attributes important to small mammals. For instance, rotten logs tend to lie flat on the ground so that animals cannot travel underneath them or pass from side to side beneath them. They also tend to lack the overhanging ledge formed by earlier decay classes and branches of freshly fallen trees. These are important aspects of hiding and escape cover provided by early decay classes of CWD (Pearson 1994; Hayes and Cross 1987). Additionally, snag densities recommended for cavity-nesting birds of 5 to 10 snags/ha (see Hunter 1990:171; Zarnowitz and Manuwal 1985; Thomas et al. 1979) are probably not sufficient to generate meaningful CWD densities on the ground. Overall, snag management guidelines designed to meet minimum requirements for cavity-nesting birds are unlikely to satisfy the CWD requirements for healthy, forest floor, small mammal populations.

Nonetheless, snag management guidelines developed for cavity-nesting birds provide insight into the complexity of this "intensive" management approach to maintaining forest structure while harvesting timber. Research on snag requirements of cavity-nesting birds has shown that diameter, height, decay class, density, context, cover type association, and species are important characteristics of snags, and different species of birds require these features to differing degrees (Raphael and White 1984; Bull 1978; Thomas et al. 1976). This has resulted in complex snag management guidelines that are based on minimum requirements identified for individual cavity-nesting birds (see Thomas et al. 1979). However, perhaps because of the complexity of these guidelines, implementation is often simplified to a general rule-of-thumb that specifies a snag density (for example, 5 to 10 snags/ha) but ignores other important snag attributes (see Hunter 1990:171). Characteristics of CWD important to small mammals are equally complex, and less information is available to guide management recommendations. Because small mammals are difficult to observe, studying their relationships to CWD attributes is costly and time-consuming. In the end, management guidelines would likely be too complex for reasonable implementation in the field. Although such research is important, a more parsimonious solution is required for effective management of CWD for small mammals.

Recommendations for Managing Snags and Coarse Woody Debris for Small Mammals—The CWD guidelines described so far are subject to the following criticisms: 1) they do not address long-term CWD recruitment; 2) they do not take into account CWD productivity based on the cover type, aspect, temperature, moisture, and other site-specific CWD determinants; and 3) they do not provide for a diverse array of CWD size classes, decay classes, and other attributes important to small mammals and other CWD-associated wildlife. Yet the importance of CWD to small mammals, their predators, and related ecological processes integral to forest ecosystems argues that CWD management for wildlife not be ignored.

A simple "within-treatment" (defined by the manager as the stand or other treatment area) Coarse Filter Approach (after Hunter 1990) could be developed to manage for CWD on the BNF and in the Northern Rockies based on an understanding of the site-specific nature of CWD recruitment. In natural systems, trees that are not entirely consumed by fire become CWD. Many become snags first. The amount of CWD on a site is determined in a very exacting manner by the number and size of trees produced there which in turn is a function of temperature, moisture, soils, and other factors specific to that site. A ponderosa pine savanna will have fewer stems, but of larger diameter than a dry-site lodgepole pine stand (Harris in press). Moist-site lodgepole pine will produce more stems that are of larger diameter, than dry-site lodgepole, but logs may decay faster. Production of CWD is cover-type and site-specific (Harris in press; Brown and See 1981). Rates of transfer from trees to snags and CWD are also site-specific, being a function of probabilities of mortality events on a site. For instance, a site may be more prone to wind-throw due to its exposure to periodic harsh winds. Other sites may be more susceptible to fire due to their position near a ridgetop where lightning-caused ignition is more frequent. Disease outbreaks may occur on a site at a higher frequency because local conditions favor the pest species.

Determining a target CWD density for small mammal habitat by cover type would be very difficult based on our current understanding of natural CWD recruitment processes (Harris in press; Brown and See 1981). Applying such a target within a cover type across a landscape would not address site-specific factors and would be an affront to managers in the sense that they would be asked to produce CWD targets on some sites that simply could not generate the target volumes. For instance, an average CWD tonnage for ponderosa pine might not be achievable on a dry site near the lower moisture limit for trees. Similarly, highly productive sites, which tend to be of greatest importance to the largest number of CWD-associated wildlife species, would not be allowed to achieve their true potential.

An effective long-term management strategy should generate CWD based on cover type and local conditions. Furthermore, distributions for CWD attributes such as length, diameter, decay, degree of branching, etc. should reflect natural distributions. These goals could be achieved by randomly assigning a portion of each tree species/cohort combination in a treatment unit to CWD recruitment. Proportions could reflect current tree composition or future tree composition based on long-term goals. For instance, in a seral ponderosa pine community, the saw timber in a stand might consist of 30 ponderosa pine and 70 Douglas-fir trees. If the proportional recruitment of CWD is to be 20 percent, then 20 trees will be assigned to CWD recruitment based on this scenario. These 20 trees could be assigned to ponderosa pine and Douglas-fir based on their proportional occurrence in the overstory (in other words, 30 percent ponderosa pine, 70 percent Douglas-fir) or all 20 could be assigned to ponderosa pine if the long-term objective is to re-establish a ponderosa pine-dominant overstory. In this manner, species composition of CWD would more quickly come to reflect that of the overstory species. Coarse woody debris recruitment must be applied to each cohort in multistory stands to provide for continuous recruitment as occurs in natural systems.

Dispersion of CWD within a stand is also important and should also reflect a random rather than uniform distribution to more closely approximate natural conditions. Trees should, therefore, be randomly assigned to CWD recruitment. Since periodic under-burning of ponderosa pine- and larch-associated cover types will likely result in some tree damage and mortality, and since this damage/mortality should be either roughly random or emulate natural fire-caused mortality, fire damaged/killed trees could contribute to CWD recruitment within fire-treated stands exhibiting such mortality. Landscapes should similarly reflect these ideas with some stands being cut while others are left as natural escapes from disturbance. Again, a random assignment of stands to harvest and non-harvest categories may best reflect natural disturbance patterns.

The idea of management priority areas could also be built into this model. For example, an area that will be managed primarily for timber harvest might be assigned 15 percent CWD recruitment, whereas an area designated for wildlife priorities could be assigned CWD recruitment at a rate of 75 percent per cohort. For intensive management areas, this essentially means that seed trees in seed tree cuts and some of the overstory in shelterwood cuts would remain on site rather than be harvested at a later date.

Assigning proportions of trees within a treatment area to CWD recruitment allows CWD to vary by cover type and local conditions that affect site productivity and decay rates. This is preferable to fixing some minimum value and forcing it onto all sites regardless of site conditions. Furthermore, natural distributions of CWD attributes should be emulated based on natural processes occurring at the treatment area. Thus, without extensive knowledge of small mammal-CWD interactions, CWD could be managed for healthy small mammal communities. Managing CWD for small mammals in this manner is preferable to setting minimum values that may not reflect the site potential or small mammal needs, given the limited knowledge of CWD-small mammal interactions. Conner (1979) noted that managing for averages instead of minimums is preferable for ecological and evolutionary reasons. I argue that the approach outlined here is ideal since it results in management for distributions that reflect natural means and variances rather than simple averages or minimums. Additionally, because of the natural linkage between CWD recruitment and snag recruitment, these guidelines can provide snags as well as logs, stumps, and root wads for a wide range of species including rare and sensitive bats, northern flying squirrels, red-backed voles, martens, fishers, salamanders, cavity-nesting birds, and mycorrhizal fungi (Bull et al. 1997).

Any successful management strategy should be founded on principles of adaptive management. The implementation of the above CWD management strategy should be monitored to assess CWD recruitment rates in different cover types. This could easily be done by permanently marking trees assigned to CWD recruitment and tracking their death and decay processes. Important questions include: 1) What percentage of trees become snags before reaching the forest floor? 2) What are the distributions of age, size, length, hardness, species, etc. of snags and CWD resulting from this approach, and how do these compare with unmanaged stands? 3) Do wildlife use these components as they do in natural stands? 4) Does the random assignment of CWD reasonably reflect natural distributions or is there a more appropriate distribution? 5) Does the CWD management strategy result in healthy forest small mammal populations? Such research would necessarily be long-term, but some of these questions would not require extensive resources once trees were marked, and long-term data collection could be built into National Forest System Monitoring programs. Proportions assigned to CWD recruitment could then be altered to adapt to new information.

Slash Treatment and Site Preparation Versus Coarse Woody Debris Retention—Minimizing the risk of fire and the negative visual impacts of logging debris through slash reduction is an important aspect of timber harvest operations. Large volumes of slash are generated through limbing, removal of tops, butts, etc. Much of this material does not qualify as CWD in terms of small mammal habitat. However, larger diameter materials (>15-cm diameter) can contribute to CWD, and material >30-cm diameter should be preserved unless volumes exceed safe fuel volumes (Reinhardt et al. 1994, 1991; Robichaud et al. 1994). Slash piling with heavy equipment is unlikely to distinguish important CWD from slash. These methods can reduce habitat for some small mammal species (Martell 1983a, 1983b). Hand piling can be used in a discriminating manner to reduce slash while maintaining CWD if crews are directed to cut and pile only materials <15-cm diameter. Broadcast burning may be the best means of reducing slash while maintaining CWD. In most cases, large diameter materials will not be removed through broadcast burning because of the time of year when such burning is done (Reinhardt et al. 1994, 1991; Robichaud et al. 1994). Slash treatments such as lop-and-scatter segment large diameter materials into short pieces. This may also have a negative impact on small mammals. Broadcast burning and piling and burning of slash <15.24 cm dia should address the negative visual effects of harvest and reduce fine fuels that serve as ignition sources while maintaining CWD.

Scarification is a commonly used technique for preparing seedbeds for larch (Arno and Fischer 1995) and ponderosa pine (D. Lockman, Biologist, Bitterroot National Forest, pers. comm.). Mechanical scarification destroys small mammal habitat (see Martell 1983a, 1983b) and deleteriously affects soils by removing woody residue (Jugensen et al. 1992). Historically, larch regenerated on burned soils, and research has shown that controlled burning works extremely well for creating larch seed beds in clearcuts, partial cuts, and even in uncut stands in western larch-Douglas-fir cover types (see Arno and Fischer 1995). Prescribed fire has less deleterious effects on small mammals than mechanical scarification and preserves organic matter for soils in larch stands (Schmidt and Shearer 1990). Prescribed fire is therefore preferable to mechanical scarification and fuels treatments. However, burned logs may not provide the same functions for small mammals as unburned logs. No research has addressed this question, but it is reasonable to assume that removal of bark, moss, branches, and fungi resulting from fire may reduce the value of CWD to small mammals for uses other than hiding and escape cover. Hand scarification practices (BNF Forest Plan 1987) are likely to impact small mammal communities and the forest floor less than mechanical scarification.

Aside from timber harvest, firewood gathering is probably the greatest threat to CWD on National Forest lands. Firewood gatherers will remove solid logs and snags from roadsides for some distance into the forest on the uphill side. The greater the road access to an area, the more critical this problem becomes. Firewood gathering restrictions must apply not only to removal of wildlife trees, but also to the removal of wildlife logs, if CWD management is to be successful.

Some economic impact will result from managing for CWD and snags since some harvestable trees will go uncut. However, long-term ecological gains are substantial. The CWD management guidelines proposed here provide large trees for seed sources, CWD for maintenance of mycorrhizal fungi and soil integrity, and visual aesthetics that will result in long-term financial gains in addition to helping achieve the long-term goals of forest health. The bottom line is, there is no other way to produce CWD and snags than to give up merchantable fiber since it is precisely this fiber that is required by wildlife, but ecosystem-level gains from managing for CWD are significant.

The Ecological Role of Douglas-fir Within Ponderosa Pine Communities

An important ecosystem management restoration goal proposed for seral ponderosa pine stands on the BNF and other Forest Service lands includes removal of Douglas-fir through harvest and controlled burning. Before such a strategy is imposed on the landscape, we should try to understand the natural ecological role of Douglas-fir within seral ponderosa pine. The presence of old Douglas-fir trees (>300 yrs) that substantially predate the period of effective fire exclusion in ponderosa pine stands demonstrates that individual Douglas-fir trees and pockets of Douglas-fir trees escaped fire in some stands (Arno et al. 1995). Additionally, our current understanding of fire intervals in these dry forest types originates from fire scar techniques that are necessarily applied to old-growth stands (Arno and Sneck 1977). These data, therefore, represent fire intervals that present a biased sample of the range of stand age classes that would have existed on the presettlement landscape. That is to say, they represent the within-stand fire interval for stands that obviously have persisted under a low intensity fire regime, in other words, natural escapes. These stands likely do not represent the full range of stands that existed on the landscape and so these data do not provide a complete understanding of presettlement fire processes at the landscape scale. Stands subjected to longer fire intervals that resulted in more intense, possibly stand-replacing fires, would not be available for sampling at the present time.

There is, therefore, little data to help explain the natural presettlement ecological role of Douglas-fir in ponderosa pine and western larch communities. However, it is reasonable to assume that even in stands that clearly underwent a fire interval of, for example, 10 to 15 years, Douglas-fir encroachment might have occurred in the form of small regenerative patches of trees somewhat younger than the average fire frequency interval, and mature Douglas-fir trees would also occur where wet sites and cool drainages within ponderosa pine stands favored escape from frequent, low-intensity fires. On the landscape scale, there were also undoubtedly entire stands that escaped fire, allowing Douglas-fir to mature and become established.

A recent study in westcentral Montana (Ruggiero and Pearson unpublished data) suggests that small mammal communities in old-growth ponderosa pine have greater species richness and evenness in stands heavily invaded by Douglas-fir than in those with very little Douglas-fir that have been treated by understory burning. Moist-site, late-seral species such as red-backed voles, red-tailed chipmunks, and vagrant shrews were found in the stands where Douglas-fir had become established in association with ephemeral drainages, adding to the diversity of small mammals present in ponderosa pine communities. Therefore, removal of encroaching fir may reduce small mammal diversity within moist ponderosa pine cover types. Some such reduction in diversity should not be a concern since it is compatible with managing for the presettlement ponderosa pine community. However, the historic role of Douglas-fir in seral ponderosa pine should be considered in light of its effect on small mammal diversity.

Small ephemeral drainages and seeps associated with some ponderosa pine stands may provide natural refugia from low-intensity fire and offer favorable habitat for Douglas-fir within ponderosa pine cover types. Red-squirrel middens are much larger and better developed in these seeps and ravines (pers. obs.), indicating the importance of these sites for this species and other small mammals that may associate with red-squirrel middens (Ruggiero and Pearson in prep.). Mesic Douglas-fir microhabitats also appeared to favor red-tailed chipmunks, red-backed voles, and shrews, which did not occur in ponderosa pine stands treated with fire and lacking in Douglas-fir (Ruggiero and Pearson unpublished data).

Douglas-fir likely historically persisted in these pockets in low numbers due to their escape from low-intensity fires. Retaining some Douglas-fir in these microsites will favor small mammal diversity and diversity of other taxa within seral ponderosa pine stands. If this is true, low intensity underburning is not a threat to Douglas-fir on these wet areas since the natural process of escape from fire will be mimicked. However, cutting could be a threat. Removal of Douglas-fir from these sites would open the canopy, thereby accelerating evaporation and greatly reducing the functionality of these oases for small mammals, plants, insects, and other species that associate with them.

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PART II - ANNOTATED BIBLIOGRAPHY

Introduction

The following annotated bibliography presents selected work on small mammal ecology and habitat use deemed most pertinent to land management on the Bitterroot National Forest. The primary focus is western Montana and the northern Rocky Mountains, but the Pacific Northwest is included for more general information and for information not currently available in the Northern Rocky Mountains.

Since I have synthesized the abstracted materials above as they pertain to the various categories reviewed, I restrict annotation here to author abstracts where possible to preserve the author's insights into the work. I provide summaries for research not abstracted. Additionally, I list study location, habitat, and key words. Habitats listed are the primary habitats presented by dominant species and successional stages reported in the study. I list key words that will best guide the reader in searching for information about the species and habitats available in a paper as it pertains to the topic of this review. These are not necessarily the "key words" presented in published works.

Annotated Bibliography

Adelman, E. B. 1979. A survey of the nongame mammals in the upper Rattlesnake Creek drainage of western Montana. Master's Thesis, University of Montana, Missoula, Montana. 129 pp.

Location: Rattlesnake Creek drainage, near Missoula, Montana.

Habitat: Cottonwood bottom, ponderosa pine, Douglas-fir, grand fir, subalpine fir, clearcut, disturbed meadow.

Keywords: Diversity, elevational gradient, habitat associations, niche breadth, niche overlap.

Abstract: During two field seasons, snap trap lines were used to determine small mammal diversity within each habitat, niche width for each mammal species, and niche overlap between species in the Upper Rattlesnake Creek Drainage, Montana. The 14 trapping locations represented 18 habitat types with varying diversities. Diversity was strongly related to elevation but was not correlated with either shrub development or tree canopy closure. Cinereus shrews, northern bog lemmings, long-tailed and meadow voles, and northern flying squirrels had the narrowest niches; red-backed voles, yellow-pine chipmunks, vagrant shrews, red-tailed chipmunks, jumping mice, and deer mice had progressively larger niches. Most species pairs did not show much, if any, niche overlap, especially when habitat abundance was considered. Mammal species diversity varied greatly from one habitat to another along a scent station line, ran twice during summer 1977, but was influenced more by the presence of the road than by habitat features. Additional mammals that visited the scent stations included golden-mantled ground and columbian ground squirrels, red squirrels, porcupines, bushy-tailed woodrats, black bears, weasels, badgers, bobcats, red foxes and coyotes. Niche overlap was moderate for most species pairs; predators did not overlap much although use tended to concentrate in a few areas. Diversity, niche breadth, and niche overlap varied between months as a result of food availability, population sizes, and hibernation.

Other species present throughout the drainage as determined from sign or mammal sightings include: pocket gophers, hoary and yellow-bellied marmots, muskrats, beavers, snowshoe hares, pikas, short- and long-tailed weasels, mink, striped skunks, wolverine, lynx, cougar, wolf, and grizzly bear.

The implications of logging, burning, recreation, and wilderness as management options are examined. The effects, both favorable and unfavorable, of these options on the different species of wildlife are summarized.

Amaranthus, M., J. M. Trappe, L. Bednar, and D. Arthur. 1994. Hypogeal fungal production in mature Douglas-fir forest fragments and surrounding plantations and its relation to coarse woody debris and animal mycophagy. Canadian Journal of Forest Research 24:2157-2165.

Location: Siskiyou National Forest, Klamath Mountains, Oregon.

Habitat: 180-year-old mature Douglas-fir, and 4, 10, 12, 14, 27-year-old plantations in clearcuts.

Keywords: Coarse woody debris, habitat associations, mycophagy, mycorrhizal fungi, truffle.

Abstract: Production of hypogeous fungi (truffles) in high-elevation, 180-year-old mature forest fragments of *Pseudotsuga menziesii* (Mirb.) Franco was compared with surrounding regenerated clearcut ranging from four to 27 years since harvest at two study areas. Thirty pairs of plots, one of each pair in soil, the other in brown-cubical-rotted coarse woody debris (CWD), were searched for truffles in each stand during four periods: August and November, 1990, and February and May, 1991. Overall analysis of presence/absence of truffles from using log-linear models revealed that CWD and mature forest status of stands each significantly influenced truffle occurrence. Mature forest fragments had greater percent frequency of occurrence and truffle number and dry weight than did plantations. The plantations did not differ significantly among each other for any parameter. CWD yielded higher numbers and biomass of truffles than soil in mature forest, but production in plantations did not differ between substrates. The total dry weight of truffles in CWD exceed that in soil by more than 10 times in mature forests. Forest practices that emphasize the retention of mature trees and coarse woody debris promote the abundance and diversity of truffles, which are integral and functionally important members of forest ecosystems.

Anthony, R. G., E. D. Forsman, G. A. Green, G. Witmer, and S. K. Nelson. 1987. Small mammal populations in riparian zones of different-aged coniferous forests. The Murrelet 68:94-102.

Location: Willamette National Forest, Oregon.

Habitat: Riparian zones of young, mature, and old-growth stands of western hemlock/Dougls-fir forests.

Keywords: Habitat associations, old growth, riparian zones, clearcutting.

Abstract: Small mammals were trapped in riparian zones in young, mature, and old-growth coniferous forests during spring and summer of 1983. *Peromyscus maniculatus* was the most abundant species and comprised 76 percent and 83 percent of the total captures during spring and summer, respectively. More species, but fewer individuals, were captured on the streamside transects in comparison to the riparian fringe transects, which were 15-20 m from the stream. Six species of Insectivora, including five species of *Sorex*, were captured in these riparian zones. No species was solely dependent on riparian zones in old-growth forests; however, additional studies are needed to define the specific habitat requirements of *Sorex bendirii*, *Sorex palustris*, *Neurotrichus gibbsii*, *Phenacomys albipes*, and *Microtus richardsoni*.

Beg, M. A. 1969. Habitats, food habits, and population dynamics of the red-tailed chipmunk, *Eutamias ruficaudus*, in western Montana. Phd, University of Montana, Missoula, Montana. 153 pp.

Location: Pattee Canyon, near Missoula, Montana; Boulder Creek, on the Flathead Indian Reservation, MT; and University of Montana Biological Station, Yellow Bay, western Montana.

Habitat: Primarily ponderosa pine and Douglas-fir forests; also western larch, Engelmann spruce and grand fir.

Keywords: Breeding, food habits, habitat associations, morphometrics, population demographics, reproduction.

Summary: M. A. Begs studied habitat use, food habits and population dynamics of the red-tailed chipmunk (*Tamias ruficaudus*) at the University of Montana Biological Station, Flathead Lake; at Boulder Creek, also near Flathead Lake; and at Pattee Canyon, near Missoula, Montana. *Tamias amoenus* inhabited two of the sites and was studied where both species occurred. *Tamias amoenus* was found in dry savanna-type habitat predominantly in ponderosa pine but also occurred in Douglas-fir (*Pseudotsuga menziesii*) where it was associated with dry exposures supporting some ponderosa pine. *Tamias ruficaudus* inhabited shady coniferous forest dominating the subalpine (*Abies lasiocarpa*) zone. In the Douglas-fir zone, where habitats intermixed to produce a mosaic, the two species maintained strict habitat segregation.

Considerable overlap was observed in diets between the two species. Examination of 158 cheek-pouches of *T. ruficaudus* and visual observations of both species in the field indicated that seeds of bull thistle (*Circium vulgare*), shrubs, and conifers and fruits were the primary foods. In the spring, when seeds were unavailable, leaves sprouts and flowers were consumed.

Populations were low in May after spring emergence and peaked in August. After August a rapid decline in populations was observed. Between-year differences were slight. Survivorship curves were calculated. Some individuals were believed to reach 7 or 8 years of age. Males moved farther than females and females moved farther than juveniles as determined by average distances moved between capture points.

Bonnell, M. L. 1967. Emergence and foraging behavior in small populations of Idaho bats. Master's Thesis, University of Idaho, Moscow, Idaho.

Location: Near Moscow, Idaho.

Habitat: Caves and mine shafts.

Keywords: Barometric pressure, food habits, foraging behavior, temperature, territoriality, threshold of illumination, relative humidity, roost habitat.

Abstract: In the summer and fall of 1966, bats belonging to the genera Myotis and Eptesicus were investigated at five roosts near Moscow, Idaho. The threshold of illumination at which bats of the genus Myotis began their foraging was shown to be 0.8 foot candles or less. *Eptesicus fuscus* emerged at 1.6 foot candles. The illumination at which bats of the genus Myotis emerged appeared to decrease slightly from August through September of 1966. Temperature and relative humidity were found to play little or no role in determining the time of evening emergence. On the nights of highest temperature, the greatest number of bats were seen. All roosts were associated with high relative humidity and running or standing water. Foraging was intermittent on the part of individual bats. Bats foraged primarily in flyways immediately adjacent to the roosts. The flight of Myotis was very erratic. These bats flew from 10 to 25 feet high. Eptesicus flew more directly and at an altitude of 100 to 200 feet. Territoriality and investigative behavior appeared to be present.

Collection of discarded insect wings beneath the roost revealed the use of Lepidoptera and Hymenoptera as food. Light sampling behavior was observed on two occasions in *Myotis evotis*. Similar behavior was induced well after foraging had begun by directing bright light sources on a mine entrance. Bats of different species were never seen to roost less then 10 feet apart.

Brown, L. N. 1967. Ecological distribution of six species of shrews and comparisons of sampling methods in the central Rocky Mountains. Journal of Mammalogy 48(4):617-623.

Location: Medicine Bow Mountains, southern Wyoming.

Habitat: Cottonwood-willow, short-grass prairie, sagebrush, mountain mahogany, aspen, lodgepole pine, spruce-fir, alpine tundra.

Keywords: Habitat associations, sampling methods, trap bias.

Abstract: The ecological distribution of six species of shrews was studied using sunken cans in 14 montane and intermountain habitats in southern Wyoming. The vagrant shrew and cinereus shrew were cosmopolitan in distribution. Cinereus shrew was slightly more abundant in moist plant communities, whereas vagrant shrew predominated in slightly drier communities. Merriam's shrew (*Sorex merriami*) occurred only in arid portions of the plains and foothills, and in short-grass prairie was the only shrew taken. The water shrew occurred only along or near cold mountain streams and ponds. The dwarf shrew (*Sorex nanus*) and the pygmy shrew (*Microsorex hoyi*) occupied restricted mountain habitats. The dwarf shrew was abundant in rocky locations in both alpine and subalpine plant communities; the pygmy shrew was taken only in peat-moss bogs in the spruce-fir zone. A comparison of snap traps and sunken cans as methods of collecting shrews revealed that snap traps failed to demonstrate the presence of *Sorex nanus* and *Microsorex hoyi* in areas where they were abundant. Also densities of *Sorex nanus* and cinereus shrew indicated by snap traps were considerably below those demonstrated by sunken cans.

Campbell, T. M., and T. W. Clark. 1980. Short-term effects of logging on red-backed voles and deer mice. Great Basin Naturalist 40(2):183-189.

Location: Bridger-Teton National Forest, Wyoming.

Habitat: Climax spruce-fir, lodgepole pine, Douglas-fir.

Keywords: Clearcut, habitat associations, logging, selective cut, small mammals.

Abstract: Clearcutting and selective logging effects on red-backed voles (*Clethrionomys gapperi*) and deer mice (*Peromyscus maniculatus*) were studied (September-November, 1975; June-October, 1976) in Bridger-Teton National Forest, Wyoming. Five selective cuts (total 137 ha) removed 57 percent (range 34 to 74 percent) of the trees. One clearcut (9.6 ha) eliminated 84 percent of the trees. Soils remained mesic in selective cuts but became xeric in the clearcut. Snap-trapping indicated that voles were most abundant on the unlogged and selectively cut mesic sites (76 percent of 408 captures), whereas deer mice were more common on the xeric clearcuts (80 percent of 60 captures). Species composition remained unchanged on selective cuts following logging (77 percent voles of 266 captures) but changed from predominantly voles to mostly deer mice (80 percent of 60 captures) in the clearcut. Intraspecific age and sex ratios, litter sizes, and morphological measurements were compared between logged and unlogged areas.

Carey, A. B., and M. L. Johnson. 1995. Small mammals in managed, naturally young, and old growth forests. Ecological Applications 5(2):336-352.

Location: Olympic peninsula, Washington.

Habitat: Old growth and managed stands (40-60 years old) of Douglas-fir/western hemlock at 85-610 m.

Keywords: Biomass, old growth, CWD, CWD management

Abstract: Forest managers in the Pacific Northwest are faced with new challenges of providing for all wildlife in managed forests. The objective was to elucidate the factors governing the composition and biomass of forest floor mammal communities that are amenable to management. Small mammal communities were sampled in forests of various management histories on the Olympic Peninsula and contrasted our results with those of other large studies in the Pacific Northwest. Forest floor mammal communities in forests >35 yr old in the Western Hemlock Zone of Washington and Oregon are composed of five to eight characteristic species. These include *Sorex trowbridgii* (numerically the most dominant); one species each of *Clethrionomys*, the *Sorex vagrans* complex, and *Peromyscus*; and *Neurotrichus gibbsii*. Species composition changes from south to north, and the communities on the Olympic Peninsula contain two or three additional species compared to communities to the south. Communities in naturally regenerated and clearcutting regenerated (managed) young forests are similar in composition to those in old growth; old growth, however, supports 1.5 times more individuals and biomass than managed forest. Community diversity seems related to the south-north moisture-temperature gradient that is reflected in increased diversity of canopy conifers, development of forest floor litter layers, accumulation of coarse woody debris, and abundance of herbs, deciduous shrubs, and shade-tolerant seedlings (as opposed to understories dominated by evergreen shrubs). Previous work found few habitat variables that were good predictors of species abundance in natural young and old-growth stands. Naturally regenerated young stands had higher levels of coarse woody debris than old growth. Managed stands had much lower abundance of coarse woody debris and tall shrubs than old growth. Understory vegetation (herbs and shrubs) and coarse woody debris accounted for a major part of the variation in abundance of six of eight species in managed stands, but only two species in old growth. Management of Western Hemlock Zone forest for conservation of biodiversity and restoration of old-growth conditions should concentrate on providing multispecies canopies, coarse woody debris, and well-developed understories.

Clarkson, D. A., and L. S. Mills. 1994. Hypogeous sporocarps in forest remnants and clearcuts in southwest Oregon. Northwest Science 68(4):259-265.

Location: Klamath Mountains, Southwestern Oregon.

Habitat: Clearcut and old-growth *Pseudotsuga menziesii / Abies concolor* forest.

Keywords: Clearcut, forest remnants, habitat associations, hypogeous sporocarp, mycophagy, mycorrhizal fungi, old growth, truffles.

Abstract: During June-August, 1991, we sampled hypogeous sporocarps on four late seral remnants ranging in size from 1.3 to 3.6 ha and on clearcuts surrounding two of the remnants. In particular our sampling of these southwestern Oregon sites (dominated by *Pseudotsuga menziesii / Abies concolor*) targeted three questions: 1) Are hypogeous sporocarps more abundant in remnants of late seral forest than in the surrounding clearcuts? 2) Are hypogeous sporocarps more abundant under coarse woody debris? 3) Is the California red-backed vole (*Clethrionomys californicus*) positively associated with areas having hypogeous sporocarps? Two forest remnants had 20-40 times more hypogeous sporocarps than the young clearcuts which surrounded them. Hypogeous sporocarps were four times more abundant in plots having logs. Voles were more likely to be caught at traps having hypogeous sporocarps nearby. Remnant stands of late seral forest appear to provide a refuge for hypogeous sporocarps used by the California red-backed vole and other small mammals, and coarse woody debris may contribute to an abundance of hypogeous fungal sporocarps.

Clothier, R. R. 1955. Contributions to the life history of *Sorex vagrans* in Montana. Journal of Mammalogy 36:214-221.

Location: Missoula Co.; Yellow Bay, Flathead Lake; Glacier National Park.

Habitat: Damp areas near water.

Keywords: Age, activity patterns, dermal glands, elevation, food habits, life history, molts, morphometrics, reproduction, associated species.

Summary: Clothier trapped 188 vagrant shrews in western Montana. These shrews and an additional 118 taken from the same areas by other collectors were examined for information on life histories. Clothier determined the age of specimens based on dental wear and assessed the variability of size with age. Based on a number of measurements taken, he concluded that only cranial height differed with age. The upper elevational limit was determined to be 6,000 feet for vagrant shrews based on unsuccessful trapping above this elevation and review of captures above 5,000 feet by other authors trapping in the area (but see earlier discussion for this species). Habitat preferences could not be determined, because the author focused only on what was believed to be prime habitat. However, his success indicates that the moist habitats trapped near streams are important for this species. Food habit results indicated that the vagrant shrew consumed primarily insects. Determination of sexual activity indicated the earliest date of pregnancy was 1 April and the latest date was 8 August. The mean number of embryos from 32 gravid females was 6.4. All but two pregnant females were born the previous year. One female showed signs of mating more than once. Mean weights of males and females was 4.7 g and did not differ between males and females in the non-reproductive season. The author found extensive habitat overlap between the vagrant and cinereus shrews, although the vagrant shrew was always more abundant. Shrews were active at all times of day and night including periods of inclement weather.

Conaway, C. H. 1952. Life history of the water shrew (*Sorex palustris navigator*). American Midland Naturalist 48(1):219-248.

Location: Missoula Co., western Montana.

Habitat: Wet sites next to streams, primarily near overhanging banks.

Keywords: Age structure, dermal glands, elevation, food habits, habitat association, life history, longevity, parasites, reproduction.

Summary: This study was based upon 119 water shrews taken in Montana, west of the Continental Divide. The majority of specimens were snap trapped along streams in the Canadian zone at elevations of 2900 to 6950 feet. All specimens were taken very close to the edges of streams and most frequently in traps placed beneath overhanging banks and within a few inches of the water. Age determination was based upon tooth-wear. No specimens lived beyond 18 months. Male water shrews were not sexually active during the breeding season in which they were born. Spermatogenesis began the following December and January, at which time an increase in body weight was apparent. All males born the previous year between January and August were in active spermatogenesis. Pregnant or lactating females were taken between February and August. Ovulation is presumably induced by copulation. A post-partum estrus occurs, and pregnancy follows in some animals. Some animals that had experienced a post-partum estrus and ovulation were not pregnant. In these individuals it is thought that reabsorption of the embryos had occurred at some stage in development. One young female was pregnant, and two others showed some ovarian activity. The majority of breeding females, however, were old animals born the preceding year. Several litters are produced during the breeding season. The modal number of embryos was six. Forty-nine percent of the stomachs examined contained immature forms of aquatic insects. Thirteen species of parasites of the water shrew were found. Dermal glands were found only in sexually active males. Two annual molts occur, one during the spring between February and May, and one in the autumn during July and August. A specimen was maintained in captivity for seven weeks. This animal was capable of capturing small minnows in the water. The average food consumption of the captive was 10.3 grams of food during a twenty-four hour period.

Fogel, R., and J. M. Trappe. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science 52(1):1-31.

Location: United States.

Habitat: Various.

Keywords: Fungi, hypogeous, literature review, mycophagy, mycorrhizae, small mammals, truffles.

Abstract: A review of the natural history literature of small mammal feeding habits, based on many fortuitous field observations, some analysis of stomach contents, and a few feeding experiments, shows that diverse animals feed on similarly diverse fungi. The interdependence of animals and fungi has evolved to a high degree in some cases. An example is the loss of alternative spore dispersal mechanisms by some fungi and the strong reliance of some mammals on fungi as a primary food. Consequently adaptation for mycophagy and the effects on mycophagy of habitat, fungal toxicity, and the food value of fungi have implications in the interpretation of ecosystem structure and function.

Foresman, K., and C. B. Henderson. 1992. Summary report: small mammal populations in harvested and mature Douglas-fir stands: Rivulet site 1991. Rocky Mountain Research Station, Forestry Sciences Lab, Missoula, MT 59812.

Location: Lolo National Forest, Montana.

Habitat: Mature and clearcut Douglas-fir stands.

Keywords: Abundance, clearcutting, management, habitat associations, community assemblages

Summary: This report presents the results of a one-year trapping study comparing the small mammal communities of mature and harvested Douglas-fir stands. Harvested plots had more individuals and a substantial increase in deer mice and red-tailed chipmunks. Long tailed voles were present on the harvested plots but not mature stands. Red-backed voles were caught on harvested plots at about the same levels as the mature stands. Their persistence may be due to the woody debris left over from logging and high shrub cover. This study supports others that find red-backed voles will use cut areas if they have not been burned.

Gashwiler, J. S. 1959. Small mammal study in West-central Oregon. Journal of Mammalogy 40(1):128-139.

Location: Central Oregon, H. J. Andrews Experimental Forest, west slope Cascade Mountains.

Habitat: Old-growth Douglas-fir, western hemlock, western red-cedar, and clearcuts in the same habitats.

Keywords: Clearcut, preliminary results, small mammal abundance, vegetation changes.

Summary: This paper presents results for the first three years of a 12-year study on the effects of clearcutting and burning on small mammal abundance and changes in vegetation in the Pacific Northwest. This paper functions as a companion paper for the following research (Gashwiler, 1970). It contains some information not present in the comprehensive review of the full 12-year study.

Gashwiler, J. S. 1970. Plant and mammal changes on a clearcut in west-central Oregon. Ecology 51(6):1018-1026.

Location: Central Oregon, H. J. Andrews Experimental Forest, west slope of the Cascade Mountains.

Habitat: Old-growth Douglas-fir, western hemlock, western red-cedar, and clearcuts in the same habitats.

Keywords: Clearcut, small mammal abundance, vegetation changes.

Abstract: Plant composition and coverage and small mammal populations were compared in virgin forest (control) and clearcut (experimental) areas from April 1954 to October 1965. Changes in ground cover vegetation were modest on the control area but marked on the experimental area. A late fall burn on the experimental area may have retarded herbaceous plant establishment. Nearly half of the herbaceous species were invaders not found in the virgin Douglas-fir (*Pseudotsuga menziesii*) forest. Ground plant coverage was less than 23 percent in the virgin forest; a year after the clearcut area was burned, the cover was 2 percent; and by 10 years it was above 53 percent. Woody plant coverage (mostly sprouts) was slightly more abundant the first two years after burning. Herbaceous species then became dominant for a 3-year period, after which woody plants gradually gained dominance. Deer mice (*Peromyscus maniculatus*) increased on the experimental area soon after the burn. The populations varied from an estimated 0.9 to 12.8 animals per acre and fluctuated widely and irregularly. Townsend's chipmunk (*Eutamias townsendii*), Oregon vole (*Microtus oregoni*) and snowshoe hare (*Lepus americanus*) also increased on the area at different periods after the burn. Trowbridge's shrew (*Sorex trowbridgii*), vagrant shrew, and ermine (*Mustela erminea*) were present on both areas in relatively low numbers. Redback voles (*Clethrionomys occidentalis*), Douglas squirrels (*Tamiasciurus douglasii*), and northern flying squirrels (*Glaucomys sabrinus*) were not found on the clearcut. California ground squirrels (*Spermophilus beecheyi*) migrated to the clearcut and established a modest population. Richardson's vole (*Microtus richardsoni*), jumping mice (*Zapus trinotatus*), bushy-tailed woodrats (*Neotoma cinerea*), and a pika (*Ochotona princeps*) were visitors.

Gunther, P. M., B. S. Horn, and G. D. Babb. 1983. Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Science 57(1): 32-44.

Location: Central Washington, western Cascade Mountains.

Habitat: Mature western hemlock, burned and unburned clearcuts.

Keywords: Food habits, habitat associations, small mammal abundance, timber management.

Abstract: Small mammals were snap-trapped in a mature conifer forest, unburned clearcuts, and burned clearcuts in the western Cascade Mountains in central Washington. The largest populations were in unburned clearcuts, and the smallest overall population was in the forest. *Sorex trowbridgii* was the most abundant insectivore caught. *Clethrionomys gapperi* was the most abundant rodent caught in most clearcuts and its population was the largest of any species in the study area. Other species caught include montane shrew, *Neurotrichus gibbsii*, *Eutamias townsendii*, *Glaucomys sabrinus*, *Peromyscus maniculatus*, *Microtus townsendii*, and *Zapus trinotatus*. Vegetation and percent cover were analyzed in the study area, and small mammal stomach contents of all nine animal species were examined. In unburned clearcuts, fungi and epiphytic lichens, especially *Alectoria sarmentosa*, and conifer seeds were the major foods eaten by rodents.

Halvorson, C. H. 1982. Rodent occurrence, habitat disturbance, and seed fall in a larch-fir forest. Ecology 63(2):423-433.

Location: Newman Ridge, western Montana.

Habitat: Clear cut and mature western larch and Douglas-fir forest.

Keywords: Clearcut, broadcast burn, habitat associations, old growth.

Abstract: Small mammal population changes were measured for five years (1970-1974) by live trapping on broadcast burned western larch (*larix occidentalis*)/Douglas-fir (*Pseudotsuga menziesii*) clearcuts and in uncut timber on a north and south slope in western Montana. Four species comprised 96 percent of the 1324 animals caught: deer mice (*Peromyscus maniculatus*) 42 percent, red-backed voles (*Clethrionomys gapperi*) 27 percent, red-tailed chipmunks (*Eutamias ruficaudus*) 22 percent, and long-tailed voles (*Microtus longicaudus*) 5 percent. Deer mice and chipmunks were common on clearcut and timber plots. The red-backed vole and long-tailed voles were associated with moist sites but showed local allopatry. The red-backed voles were present only under tree canopy and the long-tailed vole was found only in absence of tree canopy. A hard burn effect was to eliminate most of the organic mantle and small mammals except deer mice, who existed as the single species for two years, and as 80-90 percent of numbers for five postburn years. A light burn that left duff intact was associated with retention of species diversity and a low initial postburn (two years) mammal population, followed by the largest increases. Numbers of deer mice varied inversely with numbers of red-backed voles in the timber. Deer mice increased sharply on all plots the first fall after a heavy seed crop, an occurrence reported by other workers. From these pattern observations it is theorized that red-backed voles may dominate deer mice, but a heavy seed crop can temporarily enhance competitive standing of deer mice. An open xeric pioneering situation (hard burn) was conducive to consistently high deer mouse populations. The most obvious habitat feature associated with an inverse spatial relationship between the two voles was tree canopy. The long-tailed vole may be further discriminated against by drier habitats. Clearcutting appeared to be the principal determinant of total population size, but burn intensity seemed to influence species composition.

Harvey, A. E., M. J. Larsen, and M. F. Jurgensen. 1976. Distribution of ectomycorrhizae in a mature Douglas fir/larch forest soil in western Montana. Forest Science 22(4):393-398.

Location: Corum Experimental Forest, northwest Montana.

Habitat: Douglas-fir/western larch.

Keywords: Coarse woody debris, ectomycorrhizae, habitat associations, mycorrhizal fungi, prescribed burning, timber harvest.

Abstract: The top 38 cm (15 inches) of a western Montana forest soil was 60 percent mineral, 23 percent humus, 15 percent decayed wood, and 2 percent charcoal. Most (to 95 percent) of the active ectomycorrhizae were associated with the organic fractions. Five percent of all active ectomycorrhizae occurred in the mineral soil fraction, 66 percent in the humus, 21 percent in the decayed wood, and 8 percent in the charcoal. Thus, the organic reserves in this forest soil were the most important substrates for ectomycorrhizae formation. Therefore, the parent materials (leaves, litter, and woody residues) for soil organic reserves may require management during timber harvesting and prescribed burning to prevent a subsequent loss in the capacities of soils of this type (limestone base) to support ectomycorrhizal associations in mature Douglas-fir/larch forests.

Harvey, A. E., M. F. Jurgensen, M. J. Larsen, and R. T. Graham. 1987. Decaying organic materials and soil quality in the inland northwest: a management opportunity. USDA Forest Service, Intermountain Research Station General Technical Report GTR-INT-225.

Location: Inland Northwest.

Habitat: Broad range of forest cover types.

Keywords: Coarse woody debris, mycorrhizae, fungi, soil microbes, soil, litter

Abstract: Organic debris, including wood residues, provide parent materials for development and function of organic mantles on forest soils. Along with providing a storehouse of nutrients and moisture, organic materials provide either the environment or the energy source for microorganisms critical to both the nutritional quality of forest soils and the ability of conifers to extract nutrients and moisture from the soil. The role and relative importance of specific organic components can vary substantially with site and conifer species. Age of the trees appears to have less of an effect on importance of organic matter than site or species. Of the many organic materials incorporated in a forest soil, the woody component is in many ways the most important. To protect productive potential of forest soils, a continuous supply of organic materials must be provided, particularly in harsh environments. In case of excess losses of the organic mantle, complete recovery of the site may require several hundred years, even with proper management.

Hayward, G. D., and P. H. Hayward. 1995. Relative abundance and habitat associations of small mammals in Chamberlain Basin, Central Idaho. Northwest Science 69(2):114-125.

Location: Central Idaho.

Habitat: Lodgepole pine, Douglas-fir, spruce-fir, mixed conifer.

Keywords: Habitat selection, species richness, wilderness.

Abstract: We sampled small mammal populations and measured habitat structure in forested and non-forested habitats in the wilderness of central Idaho over a 5-year period using pit and snap traps. Although results from pit and snap trapping differed for northern pocket gophers (*Thomomys talpoides*), capture rates for the two methods were similar across habitats for the other common species. Southern red-backed voles (*Clethrionomys gapperi*) and shrews (*Sorex vagrans* and *S. cinereus*) were the most common species captured. Spruce-fir forests exceeded other habitats in the abundance of small mammals while all sites had low species richness (s = 4.7). Habitat association of the common small mammals (southern red-backed voles, shrews, deer mice (*Peromyscus maniculatus*) and yellow-pine chipmunks (*Tamias amoenus*)) differed, based on both broad patterns and microhabitat gradients. Our data corroborate the results of other investigations by demonstrating the relatively low abundance of small mammals in subalpine habitats of the Rocky Mountains. Furthermore, the differences in small mammal communities among forest types suggests a mosaic pattern of small mammal communities in the Rockies that results from the patchy nature of forests in this region.

Hoffman, G. R. 1960. The small mammal components of six climax plant associations in eastern Washington and northern Idaho. Ecology 41(3): 571-572.

Location: Eastern Washington and northern Idaho

Habitat: *Pinus ponderosa, Pseudotsuga menziesii, Thuja plicata,* and *Tsuga heterophylla* forests

Keywords: Habitat associations, small mammals

Summary: Small mammals were trapped in six plant associations (*Pinus ponderosa-Agropyron spicatum, Pseudotsuga menziesii-Calamagrostis rubescens, Thuja plicata / Tsuga heterophylla-Pachistima myrsinites, Thuja plicata / Tsuga heterophylla-Oplopanax horridum, Alnus sinuata*, and *Carex lasiocarpa*) in eastern Washington and northern Idaho. The deer mouse and vagrant shrew were most widespread, being found in four and five of the six plant associations, respectively. The deer mouse was abundant in *Pinus ponderosa-Agropyron spicatum* savanna and the only small mammal of 11 species trapped to be found in this habitat. Vagrant shrew was similarly the only species taken in the *Pseudotsuga menziesii-Calamagrostis rubescens* habitat, but only one individual was taken. Cinereus shrew was taken only in *Thuja plicata / Tsuga heterophylla-Pachistima myrsinites* habitat. *Phenacomys intermedius* and *Tamias amoenus* were taken only in *Thuja plicata-Tsuga heterophylla* associations. Only one *Tamias ruficaudus* was taken. This individual was captured in the *Alnus sinuata* community. Two *Clethrionomys gapperi* were taken in the *Thuja / Tsuga-Oplopanax* habitat and nine were taken in the *Alnus sinuata* association. *Zapus princeps* and *Microtus montanus* were taken only in the *Alnus sinuata* association. *Microtus pennsylvanicus* was the most abundant species trapped, but all individuals were found in the *Carex lasiocarpa* habitat. The *Thuja plicata / Tsuga heterophylla-Pachistima myrsinites, Thuja plicata / Tsuga heterophylla-Oplopanax horridum* and *Alnus sinuata* were the most diverse habitats having six, five, and six species each, which were fairly evenly represented. This was true even though the *Thuja plicata / Tsuga heterophylla-Oplopanax horridum* association was under-trapped relative to the others. The *Carex lasiocarpa* habitat contained only two species but had the greatest number of captures due to the abundance of vagrant shrew and *M. pennsylvanicus* found in this habitat. The *Pinus ponderosa-Agropyron spicatum* and *Pseudotsuga menziesii-Calamagrostis rubescens* associations were relatively depauperate.

Hoffmann, R. S., P. L. Wright, and F. E. Newby. 1969. The distribution of some mammals in Montana. I. Mammals other than bats. Journal of Mammalogy 50(3):579-604.

Location: Montana.

Habitat: Various.

Keywords: Distribution, habitat associations.

Abstract: Information on current distribution of 40 species of mammals in Montana is given. Four species, Preble's shrew, *Sciurus niger*, *Perognathus parvus*, and *Procyon lotor* are reported for the first time in Montana.

Key, C. H. 1979. Mammalian utilization of floodplain habitats along the North Fork of the Flathead River in Glacier National Park, Montana. Master's Thesis, University of Montana, Missoula, Montana. 151 pp.

Location: Northwest Montana, North Fork Flathead River, Glacier National Park.

Habitat: Riparian including spruce and cottonwood dominated forest.

Keywords: Floodplain, habitat utilization, small mammal abundance, succession.

Abstract: Mammalian communities on the North Fork of the Flathead River Floodplain in Glacier National Park were investigated during 1976 and 1977 to provide baseline data on the small mammal fauna, to evaluate the importance of floodplains to medium-sized carnivores, and to establish monitoring procedures so that park resource managers might better assess the future impact of human disturbance. Six permanent plots were established from which estimates of small mammal distribution and abundance can be made in future years. Floodplains were productive areas for small mammals. Twelve species were captured. Both density and biomass were greater in frequently flooded habitats than in most other types, including adjacent communities not subject to periodic flooding. Young seres were characterized by low species diversity and high relative abundance of deer mice. Older coniferous seres supported more species, but total abundance, though similar to early seres in some cases, was more equally distributed between the species present. Statistically significant differences existed in small mammal densities between study plots but decreased significantly the second field season when total small mammal density was low.

A plea is made to exercise great care when interpreting data from floodplain plots due to the high degree of natural variation in small mammal abundance. The mere density of a small mammal species would represent a good indicator of human disturbance. Given slight inter-plot variation, species diversity may be the best indicator of community change, provided the analysis controlled for expected variation due to changes in total small mammal density. Several small predators frequented floodplains, which provided access to prey, shelter, and travel routes. Otter and mink, linked directly to the aquatic system, would be good indicators of water quality changes and easily censused if utilized in environmental monitoring. Additional baseline data are needed on those species as a prerequisite to monitoring, however.

Landres, P, D. Spildie, and R. Lee. 1995. Progress Report: Bitterroot Ecosystem Management - small mammal report. Submitted to Rocky Mountain Research Station, Missoula, MT.

Location: Headwaters of Smith Creek, Selway-Bitterroot Wilderness, Bitterroot National Forest.

Habitat: Habitat is not given. Clearcut; burn; uncut stand adjacent to clearcut and burn treatments; and control within contiguous stand in wilderness.

Keywords: Disturbance, fire, populations estimates, preliminary report, species composition, timber harvest.

Abstract: This is a preliminary report presented by the authors to briefly summarize initial results. The goals of the project were to 1) determine whether "timber harvesting or fire disturbances influence the species composition and population densities of small mammal communities on adjacent but undisturbed sites" and 2) determine "what are the effects of timber harvest and fire disturbances on species composition and population densities of small mammal communities that were similar before these disturbances?" The preliminary conclusion was drawn that no effect from burn or clearcut was observed in small mammal populations in the stand adjacent to the two types of disturbance.

Lee, S. D. 1995. Comparison of population characteristics of three species of shrews and the shrew-mole in habitats with different amounts of coarse woody debris. Acta Theriologica 40(4):415-424.

Location: Fort Lewis Military Reservation, Pierce county, Washington.

Habitat: 50-60 year old Douglas-fir/western hemlock forests.

Keywords: Coarse woody debris, habitat associations, population dynamics, reproductive rates

Abstract: Seasonal fluctuation and its causes for three species of *Sorex* shrews and the shrew-mole *Neutrichus gibbsii* Baird, 1857 were investigated in three sites with high amounts of coarse woody debris (CWD) and three sites with low amounts of CWD in managed forests of western Washington, USA. *Sorex trowbridgii* Baird, 1857 was more abundant on sites with high amounts of CWD (captures per 100 trapping nights) and had higher reproductive rates than in sites with low amounts of CWD. *Sorex monticolus* Merriam, 1890 showed higher reproductive rates on sites with high amount of CWD. Population of *Sorex vagrans* Baird, 1857 fluctuated greater and abundance was higher in sites with low amounts of CWD. Most reproduction occurred from January to April and declined rapidly in May. Previous studies also have shown an early onset of breeding in Coastal California and Oregon. It seems that local species of soricids and *Neutrichus gibbsii* gain reproductive benefits by breeding primarily in January through May.

Luoma, S. N. 1970. A study of hibernation in the western jumping mouse, *Zapus princeps*. Master's Thesis, Montana State University, Bozeman, Montana.

Location: Western Montana.

Habitat: High elevation grassy meadows; laboratory.

Keywords: Brown fat, hibernation, torpor, weight gain, weight loss.

Abstract: A field and laboratory study of hibernation in *Zapus princeps* was conducted. Males gained weight more gradually and reached a higher peak than female *Z. princeps*. Hibernation was preceded in all animals by a period of lethargy and weight loss during which body temperatures were very labile. Torpor was easily induced during the summer by removing either food or water at any temperature below 22C. Arousal from induced torpor during the summer did not occur at temperatures below 10C, probably due to lack of a sufficient amount of brown fat. Animals kept at constant temperature (3±1C) in 24 hours of light per day hibernated two to three weeks earlier than animals caged outside. The characteristics of hibernation in *Z. princeps* appear to place it between the large obligatory hibernators and the smaller mammals that hibernate.

Malloy, J. C. 1981. The effects of 1080 baiting on columbian ground squirrels and nontarget mammal and bird populations. Master's Thesis, University of Montana, Missoula, Montana. 65 pp.

Location: Blackfoot Valley, western Montana.

Habitat: Grasslands.

Keywords: Nontarget mortality, pesticide, populations estimates, rodent control, 1080 baiting.

Abstract: Target and nontarget mortality from 1080 baiting of columbian ground squirrels (*Spermophilus columbianus*) was investigated in the Blackfoot Valley of western Montana. Ground squirrel population estimates declined to 0 on the treatment area immediately after poisoning but returned to approximately 20 percent of their former levels within 1 year after treatment. Immigrants apparently came from the nearest untreated site, less than 246 feet (75 m) away. Juvenile squirrels were disproportionately less abundant on the treatment area in 1980 than in 1979, the treatment year. Capture rates and population estimates for small mammals declined immediately after baiting on the treatment area and increased on the control area. Population estimates declined further over the following winter on both treatment and control areas and reached a low point in the spring of 1980. The over-winter decline was greater than the decline following baiting and was presumably a natural fluctuation. Passerine bird population indices varied after baiting but not in a manner attributable to the poisoning campaign. Granivorous birds were apparently unaffected by 1080 baiting. Three common raven (*Corvus corax*) carcasses were recovered. Carnivore populations were not reliably surveyed. Scent station indices and carcass recoveries indicated that coyote (*Canus latrans*) mortality occurred, but the magnitude of population reduction was not quantifiable. Post-treatment observations indicated that coyotes and other carnivores were not extirpated, even on treated areas. Carcass recovery indicated that mortality may be locally high where coyotes are traditional users of a treated area. Toxicity testing suggested that coyotes could easily acquire a lethal dose of squirrel carcasses, but because of their high tolerance levels, badgers (*Taxidea taxus*) and Golden Eagles (*Aquila chrysatos*) would seldom eat lethal amounts before carcass decomposition or removal by other species. Monitoring of rodent carcasses available aboveground showed that such carcasses were available to scavengers for less than two weeks after baiting.

Maser, C., J. M. Trappe, and R. A. Nussbaum. 1978. Fungal small mammal interrelationships with emphasis on Oregon coniferous forests. Ecology 59(4):799-809.

Location: Oregon.

Habitat: Various.

Keywords: Food habits, hypogeous mycorrhizal fungi, mycorrhizal symbiosis, spore dispersal, rodent mycophagy.

Abstract: Most higher plants have evolved with an obligatory symbiotic relationship with mycorrhizal fungi. Epigeous mycorrhizae formers have their spores dispersed by air currents, but hypogeous mycorrhizal fungi are dependent upon small mammals as primary vectors of spore dissemination. Mammalian mycophagists defecate within the coniferous forest ecosystem, spreading the viable spores necessary for survival and health of the conifers. As one unravels and begins to understand the interrelationships between small mammals mycophagists and mycorrhizal fungi, it becomes apparent that the various roles of small mammals in the coniferous forest ecosystem need to be reevaluated. One can no longer accept such simplistic solutions to timber management as poisoning forest rodents to "enhance" tree survival. One must consider the direct as well as the indirect costs and benefits of timber management decisions if one is to maintain balanced, healthy coniferous forests.

Maser, Z., C. Maser, and J. M. Trappe. 1985. Food habits of the northern flying squirrel (*Glaucomys sabrinus*) in Oregon. Canadian Journal of Zoology 63:1084-1088.

Location: Northern Oregon

Habitat: Old-growth Douglas-fir, old-growth lodgepole pine, mixed conifer forests including grand fir, Engelmann spruce, and western larch; and some ponderosa pine forests.

Keywords: Food habits, hypogeous fungi, mycophagy, mycorrhizal symbiosis, spore dispersal, stomach content analysis.

Abstract: Digestive tracts of 91 northern flying squirrels (*Glaucomys sabrinus*) were analyzed for food items; 28 were from northwestern Oregon and 63 from northeastern Oregon. Ninety percent or more of the ingested materials were fungi and lichens, including 20 genera of hypogeous fungi. The northern flying squirrel, in using hypogeous fungi as a major food source, is an important nocturnal disperser of the spores. In Oregon coniferous forests, these fungi are obligatory ectomycorrhizal symbionts with the trees in which the squirrels live.

Maser, C., Z. Maser, J.W. Witt, and G. Hunt. 1986. The northern flying squirrel: a mycophagist in southwestern Oregon. Canadian Journal of Zoology 64:2086-2089.

Location: Southwestern Oregon.

Habitat: Douglas-fir/western hemlock/western red cedar.

Keywords: Dietary specialist, fecal analysis, food habits, fungi, hypogeous sporocarps, mycophagy.

Abstract: Fecal samples were collected over 27 months from the northern flying squirrel (*Glaucomys sabrinus*(Shaw)), a mycophagist in the Pacific Northwest portion of its range. Nine genera of hypogeous Basidiomycetes, 10 of hypogeous Ascomycetes, and one of hypogeous Zygomycetes were identified from fecal samples (hypogeous fungi fruit underground). The squirrel food habits generally paralleled the seasonal availability of the hypogeous fungi, but with notable exceptions. Our data demonstrate the functional diversity an individual species lends to its habitat when viewed in a functional context.

McCracken, K. E. 1990. Microhabitat and dietary partitioning in three species of shrews at Yellow Bay, Montana. Master's Thesis, University of Montana, Missoula, Montana. 38 pp.

Location: University of Montana, Biological Station, Yellow Bay, Flathead Lake, western Montana.

Habitat: Mature grand fir forest.

Keywords: Competition, food habits, logs, habitat use, mature forest, mesic, xeric.

Abstract: Habitat use patterns and food habits of three species of shrews (vagrant shrew, cinereus shrew, and montane shrew) were analyzed in a grand fir (*Abies grandis*)/queencup beedlily (*Clintonia uniflora*) habitat in northwestern Montana. Distribution of the three species differed significantly across mesic and xeric sites, with vagrant shrew captures being most numerous on the mesic site and cinereus shrew captures more numerous on the xeric site. The montane shrew, at its lower elevational range, was infrequently captured on both plots. Thirty-five live-trapped vagrant shrew and cinereus shrew were marked with phosphorescent dust and released at their site of capture. Mapping of individual's movements revealed no discernable differences between species, but the most conspicuous habitat component used by both was the space between fallen trees (decomposition classes 1-3) as runways. Microhabitat used by the three species was investigated using multivariate analysis of 15 trapsite characteristics. There were significant differences between vagrant shrew and cinereus shrew on five variables, and between vagrant shrew and montane shrew on one variable. These results suggest that vagrant shrew and cinereus shrew partition the space within the habitat at both large and small scales. Habitat segregation may be due to asymmetric competition between the two species, involving interference competition, exploitative competition, or both.

Summer foods of the three species (20 vagrant shrew, 10 cinereus shrew, and four montane shrew) were examined using stomach contents. Major foods in order by percent frequency were vagrant shrew: ants, true flies, beetles, and adult lepidopterans; cinereus shrew: ants, adult lepidopterans, beetles, and spiders; montane shrew: ants, spiders, true flies, and millipedes. No significant difference in prey items consumed was observed among the three species. These data indicate that, at the taxonomic level of Order, there is a high degree of overlap in foods among the three species. However, they could be separating food on the basis of prey size, foraging method, or at a lower taxonomic level.

Medin, D. E. 1986. Small mammal responses to diameter-cut logging in an Idaho Douglas-fir forest. USDA Forest Service, Intermountain Research Station, Research Note, INT-362.

Location: West-central Idaho.

Habitat: Douglas-fir and ponderosa pine dominate with some grand fir lodgepole pine and Engelmann spruce.

Keywords: Composition changes, diameter-cut logging, population changes.

Abstract: Relative small mammal populations were estimated on logged and unlogged plots from 1975 (first year prelogging) through 1979 (third year post-logging) by using live-trapping and mark-recapture methods. Three species made up 93 percent of 698 individual animals caught: deer mice (*Peromyscus maniculatus*), yellow-pine chipmunks (*Tamias amoenus*), and Gapper's red-backed voles (*Clethrionomys gapperi*). Deer mice populations were similar on both logged and unlogged plots. Numbers of yellow-pine chipmunks increased on logged sites. Red-backed voles disappeared from the small mammal community after logging. Other species including the golden-mantled ground squirrel (*Spermophilus lateralis*) and shrews (*Sorex* spp.) were trapped irregularly and in smaller numbers.

Medin, D. E., and G. D. Booth. 1989. Responses of birds and small mammals to single-tree selection logging in Idaho. USDA Forest Service, Intermountain Research Station, Research Paper, INT-408.

Location: West-central Idaho.

Habitat: Douglas-fir and ponderosa pine dominate with some grand fir lodgepole pine and Engelmann spruce.

Keywords: Composition changes, population changes, single-tree selection logging.

Summary: Responses of birds and small mammals to logging depends on the cutting methods used and the degree to which forest stands are altered. This study examined short-term changes in the composition and abundance of small mammals and breeding birds following single-tree selection logging in an Idaho Douglas-fir forest. Populations of birds and mammals were estimated on a logged plot and on a nearby unlogged plot from 1975 (two years prelogging) to 1979 (three years post-logging). Total numbers of breeding birds were relatively stable between years and between logged and unlogged plots. More pronounced patterns of response occurred in the populations making up the breeding bird communities. Species with positive numerical responses to the selection cut were olive-sided flycatcher, Swainson's thrush, yellow-rumped warbler, and chipping sparrow. Species with negative numerical responses to logging were red-breasted nuthatch and brown creeper. Fourteen other species showed little numerical response to the timber harvest. Birds that forage by gleaning the surface of the bark (timber gleaners) declined in number after logging. Foliage feeders, aerial-sally feeders, and timber drillers were about equally abundant before and after logging. The ground gleaning guild showed a slightly positive pattern of response. Of six nesting guilds represented only the secondary cavity nesters were adversely affected by logging. Bush and small tree nesters tended to increase after timber harvest. Deer mice, yellow-pine chipmunks, and boreal redback voles accounted for 93 percent of 815 individual animals trapped during the study. Postlogging estimates of deer mice density were generally similar on both the logged and the unlogged plots. But when results were expressed as the mean number of individual animals trapped each year, significantly fewer deer mice were trapped on the logged plot. Numbers of yellow-pine chipmunks increased on logged sites; it was the most commonly trapped small mammal in postlogging environments. No significant difference was found in the number of red-backed voles trapped in the cut and uncut forest. Other species were trapped irregularly and in smaller numbers.

Metzgar, L. H., Pearson, D. E., and P. Todd. 1990. Teller Wildlife Refuge wildlife assessment and recommendations. Wildlife Biology Program, University of Montana, Missoula Montana. 111 pp.

Location: Western Montana, Teller Wildlife Refuge, Bitterroot Valley.

Habitat: Riparian cottonwood (*Populus tricocarpa*) and ponderosa pine (*Pinus ponderosa*) and some upland grasslands.

Keywords: Habitat assessment, species inventory, management recommendations.

Summary: This document presents the results of a wildlife inventory on the Teller Wildlife Refuge, near Corvallis, Montana. Management recommendations were made for wildlife habitat improvement in seven areas: habitat; fish and aquatics; waterfowl; nongame and upland game birds; small mammals; carnivores and fur bearers; deer. Includes species lists and maps.

Morris, D. W. 1984. Patterns of scale and habitat use in two temperate zone small mammal faunas. Canadian Journal of Zoology 62:1540-1547.

Location: Rocky Mountains, southern Alberta, Point Pelee National Park, southern Ontario.

Habitat: Clearcut to climax mature forest in white spruce, Douglas-fir, subalpine fir.

Keywords: Clearcut, habitat use, macrohabitat, microhabitat, scale, succession.

Abstract: Small mammals were livetrapped and habitat quantified in replicates of six macrohabitats in Alberta and in temporal replicates in four macrohabitats in Ontario, Canada. Similar patterns emerged in both locations. The relative abundances of small mammals depended upon macrohabitat; within macrohabitats, species differed significantly in microhabitat use. The patterns were dynamic and probably the result of habitat preferences instead of species interactions. Macrohabitat differences may in part be outcomes of microhabitat selection but are unlikely to be completely understood without superimposing colonization and extinction probabilities on habitat selection models. Field biologists must recognize both scales of habitat to interpret patterns of species distribution.

Nordyke, K. A., and S. W. Buskirk. 1991. Southern red backed vole, *Clethrionomys gapperi*, populations in relation to stand succession and old growth character in the central Rocky Mountains. Canadian Field-Naturalist 105(3):330-334.

Location: Southeastern Wyoming, Medicine Bow Mountains.

Habitat: Lodgepole pine stands and Engelmann spruce/subalpine fir stands representing early-seral, mid-seral and old-growth conditions.

Keywords: Log decay, old-growth indicator species, old-growth rating, successional stage.

Abstract: The effects of old-growth character, microhabitat characteristics, and successional stage on the Southern Red-backed vole (*Clethrionomys gapperi*) were investigated in conifer forests of southeastern Wyoming in 1986 and 1987. Small mammals were snap-trapped in Lodgepole Pine, mature spruce-fir, and old-growth spruce-fir habitat types. Vole abundance was greatest and body condition best in old-growth spruce-fir. Vole captures best fit a second-degree polynomial model when regressed on old-growth rating in 1987; understory cover followed a similar pattern with rating. Abundance was positively correlated with understory cover both years, and because of this relationship and the binomial response of both of these to old-growth rating, understory cover may influence distribution of *C. gapperi* more than do other habitat features. Vole abundance was positively correlated with stage of decay of logs.

Pattie, D. L. 1967. Dynamics of alpine small mammal populations. Ph.D. Dissertation, University of Montana, Missoula, Montana. 103 pp.

Location: Beartooth Pass, Montana-Wyoming boarder.

Habitat: Krummholz whitebark pine and subalpine fir; alpine.

Keywords: Activity patterns, demographics, habitat associations, home range, population density.

Abstract: A study to determine characteristic of alpine populations of *Peromyscus maniculatus, Microtus montanus* and *Arvicola richardsoni* was centered near Beartooth Pass on the Montana-Wyoming border at an elevation of 10,500 ft. A 3-day visit in late December 1963 and another during late August 1965 supplemented information collected during 350 days spent in the field during the summers of 1961-1964. Data were collected by both snap and live trapping. Numbers and species of all mammals trapped are listed; a general description of the communities, geology, and topology of the plateau is given. Characteristics described for the three species include estimated of density and movement, home range, activity patterns, and sex ratios. Habitat distribution of the species, reproductive patterns, and mortality factors are also considered. Similar information is given for other alpine mammals if sufficient data were available. The absence of cyclic population fluctuations was considered in the light of both extrinsic and intrinsic factors. It is postulated that the absence of cycles in the alpine is related to extrinsic factors that prevent buildup of populations to levels where intrinsic factors such as stress may operate to limit reproduction and thus produce a decline in numbers.

Pearson, D. E. 1994. Habitat use by the southern red backed vole (*Clethrionomys gapperi*): response of an old-growth associated species to succession. Master's Thesis, University of Montana, Missoula, Montana. P. 105.

Location: Lake McDonald Valley, western Montana, Glacier National Park.

Habitat: Western red-ceder/western hemlock forests dominated by lodgepole pine in the youngest stands. Includes four age classes: 65, 138, 256 and 457 years.

Keywords: Competition, habitat generalist, habitat specialist, macrohabitat selection, microhabitat selection, old-growth associate, successional stages.

Abstract: Populations of the southern red-backed vole (*Clethrionomys gapperi*) and deer mouse (*Peromyscus maniculatus*) were examined in four successional stages (65, 138, 256, 457 years) in cedar-hemlock (*Thuja plicata-Tsuga heterophylla*) forests of Glacier National Park to determine macrohabitat selection among stands and microhabitat selection within stands. Abundance of *Clethrionomys gapperi* and *Peromyscus maniculatus* increased with increasing stand age. Microhabitat use differed from available habitat for both species within most age classes but was not consistent for either species among age classes. The inconsistency in microhabitat use among successional stages and lack of correspondence between micro- and macrohabitat variables selected leads to the conclusion that macrohabitat associations determine microhabitat selection. In order to properly assess habitat use at either scale, the difference between scales must be addressed in the design and analysis of habitat studies. *Peromyscus maniculatus* behaved as a generalist at the macrohabitat scale but exhibited stronger microhabitat selection than did *C. gapperi. P. maniculatus* may exhibit "habitat switching" and respond to local site conditions by developing search images that manifest themselves as distinctive foraging patterns at the microhabitat scale. Such behavior would render *P. maniculatus* a potentially formidable competitor for resources and explain its tenacity for a wide variety of habitats. *Clethrionomys gapperi* exhibits a strong positive linear relationship with stand age and old-growth conditions near the forest floor. If monitored in conjunction with other species such as the pine marten (*Martes americana*), pileated woodpecker (*Dryocopus pileatus*) and barred owl (*Strix asio*), *C. gapperi* could contribute significantly to an "indicator guild" for identifying and monitoring the old-growth condition. Fluorescent pigment tracking and live trapping were compared to determine microhabitat use by *Clethrionomys gapperi*. The two methods generally agreed, but fluorescent pigment tracking may allow more sensitive analyses of microhabitat use.

Pearson, D. E. 1991. The northern bog lemming in Montana and the contiguous United States: distribution, ecology, and relict species theory. Senior Thesis, University of Montana, Missoula, Montana. 33 pp.

Location: Western Montana.

Habitat: Bogs, fens and wet meadows.

Keywords: Bog lemming survey, habitat associations, literature review, sensitive species, sphagnum bogs.

Abstract: The northern bog lemming is a rare mammal in the contiguous United States. This paper presents results from a distributional study of the species in Montana. Results from a literature review of trapping data from the contiguous United States are also presented. Additionally, the northern bog lemming's status with regard to relict species theory is examined.

Ramirez, P. Jr., and M. Hornocker. 1981. Small mammal populations in different-aged clearcuts in northwest Montana. Journal of Mammalogy 62(2):400-403.

Location: Northwest Montana, Sullivan and Quintonkon Creek drainages of the South Fork Flathead River.

Habitat: Subalpine fir-clintonia and subalpine fir-woodrush habitat types.

Keywords: Clearcut, habitat associations, uncut forest, small mammal abundance.

Summary: Small mammals were sampled in clearcut and uncut stands of *Abies lasiocarpa-Clintonia uniflora* and *Abies lasiocarpa-Luzula hitchcockii* habitat types using snaptraps for all but *Spermophilus columbianus*, for which wiremesh traps were used. *Peromyscus maniculatus* densities were higher in 5-year-old clearcuts than in older clearcuts or uncut forest. *Clethrionomys gapperi* densities were highest in *Abies-Clintonia* and *Abies-Luzula* uncut forests than in clearcuts. *Spermophilus columbianus* were most abundant in clearcuts of all ages (5-15 years old).

Raphael, M. G. 1988. Habitat associations of small mammals in a subalpine forest, southeastern Wyoming. Pp. 359 - 367. In Management of amphibians, reptiles and small mammals in North America. Symposium, Flagstaff, AZ.

Location: Southcentral Wyoming.

Habitat: Lodgepole pine and Engelmann spruce-subalpine fir.

Keywords: Ecological indicator, habitat associations, old-growth forest.

Abstract: Mammal capture rates were greatest at sites with mature timber and other old-growth attributes. Shrews (both dusky (*Sorex monticolus*) and masked (*S. cinereus*)) and southern red-backed voles (*Clethrionomys gapperi*) were much more abundant at sites dominated by spruce or fir compared to dryer sites dominated by lodgepole pine. Deer mice (*Peromyscus maniculatus*), in contrast, were most abundant on dryer pine-dominated sites. The southern red-backed vole, because of its high abundance and strong association with mature forest, is a good ecological indicator of late seral conditions for forest planning purposes.

Reichel, J. D., and S. G. Beckstrom. 1994. Northern bog lemming survey. A report to the USDA Forest Service, Kootenai National Forest, Flathead National Forest, and Lewis and Clark National Forest. Montana Natural Heritage Program, Helena, Montana. P. 87.

Location: Western Montana.

Habitat: Bogs, fens and wet meadows.

Keywords: Annotated bibliography, bog lemming survey, bogs, moss mats, sensitive species.

Abstract: During the 1993 field season we surveyed for small mammals at 30 sites, catching northern bog lemmings at five new sites. One site, Wood Creek on the Rocky Mountain Ranger District, Lewis and Clark National Forest, is the eastern-most site known in Montana and 90 km from the nearest previously known site. Three sites on the Kootenai National Forest were in the Sunday Creek drainage, 1-6 km from the site discovered there in 1992. The last new site, also in the Kootenai National Forest, was found at Cody Lake, 32 km from the nearest known site. Despite surveys at 5 sites with apparently good-excellent habitat on the Flathead National Forest, no new lemming sites were found there. The total number of known bog lemming sites in Montana is 17, the most sites in any of the lower 48 states. All sites found during 1993 had moss mats at or near the trap location. Known sites in Montana range in size from one to approximately 340 acres. The habitat predictor for potential northern bog lemmings sites in Montana is the presence of large, thick moss mats, particularly sphagnum moss. More sites with apparently good quality habitat were trapped unsuccessfully in 1993 than in 1992; whether lemmings are actually present at some or all of those sites is unknown.

Reichel, J. D., and S. G. Beckstrom. 1993. Northern bog lemming survey 1992. A report to the USDA Forest Service, Kootenai National Forest. Montana Natural Heritage Program, Helena, Montana.

Location: Western Montana.

Habitat: Bogs, fens and wet meadows.

Keywords: Bog lemming survey, bogs, management recommendations, moss mats, sensitive species.

Abstract: This document provides a preliminary report on results from a survey for bog lemmings conducted in western Montana by the Montana Natural Heritage Program. Reichel and Beckstrom report on five new sites for the northern bog lemming in Montana. These sites were Hawkins Pond, Sunday Creek, and Bowen Creek in northwest Montana, and Meadow Creek and Maybee Meadows in southwestern Montana. The Meadow Creek site is on the BNF. The Maybee Meadows site is the southern-most extent of the northern bog lemming's range in the western US. The authors discuss the potential importance of sphagnum mats in bog-like habitats and provide management recommendations for protecting this rare microtine.

Roemer, D. M. 1994. Results of field surveys for bats on the Kootenai National Forest and the Lolo National Forest of western Montana, 1993. Montana Natural Heritage Program, Helena, Montana. 19 pp.

Location: Western Montana, Kootenai and Lolo National Forests.

Habitat: Primarily moist forests.

Keywords: Bats, bat detectors, echolocation, mist netting, survey.

Summary: This report documents the findings of field investigations into the relative abundance and distribution of bats on the Kootenai National Forest and parts of the Lolo National Forest of western Montana from May 15 to September 28, 1993. Two primary methods of investigation of species composition and abundance were used. Bat echolocation calls were monitored along selected transect routes beginning at sunset to record the relative abundance and activity patterns of bats. Mist nests were deployed across creeks, roads, trails, and adits to capture bats, providing the most reliable means for documenting species presence, and providing information of age, sex, and reproductive status. A total of 123 bats representing eight species were captured in the study area. Bats of the genus *Myotis* accounted for 91 percent of all captures. *M. lucifugus* was captured most frequently (48 percent), followed by *M. californicus* (15 percent), *M. evotis* (13 percent), *M. volans* (8 percent), *Lasionycteris noctivagans* (7 percent), and *M. ciliolabrum* (7 percent). One specimen each of *Plecotus townsendii* and *Lasiurus cinereus* were captured, comprising less than one percent of the total capture. Relative bat abundance varied greatly between 24 sites monitored during the study. High levels of bat activity were found at Camp 32 (74 passes/hr), Upper Fortine Creek (72 passes/hr), and Trout Creek (60 passes/hr). Sites demonstrating the most foraging activity as measured by feeding buzzes per hour were Camp 32 (n=29), Big Creek (n=14), and Bull Lake (n=13). The mean index of bat activity at the 24 transect locations was 33.5 = 8.9 passes per hour, and 6.3 = 2.7 feeding buzzes per hour ($\bar{x} = 0.025$). Bats were regularly encountered foraging over roads, creeks, and ponds in the study area. Of 1,031 bat passes detected at 24 transect locations, 19 percent (n=196) were attempting to capture prey. Foraging activity was highest at Camp 32 where 43 percent of bats passes contained a feeding buzz. Foraging bats were absent at three sites in the study area but comprised at least 8 percent of all bat passes at every other site. Two adits investigated during this study were utilized by bats as night roosts. *Myotis evotis* were captured at the entrances of two adits on the Superior Ranger District. The Trout creek adits, located on the west side of Trout Creek at approximately 3800' and 4100' elevation, were visited by male and female *M. evotis* on 13 July. The lower adit contained bat guano and culled moth wings. Only three juvenile bats (2 percent) were captured during the study—two male *M. lucifugus* at Lower Fortine Creek on 29 August, and one female *M. volans* at Rock Creek on 27 September. Females comprised 62 of 120 adults captured in mist nets (52 percent). Lactating *M. Lucifugus, M. californicus, M. ciliolabrum*, and *M. evotis* were captured during the study between 15 July and 1 September. Lactating females represented 7 percent of the total bats captured, and 13 percent of adult female bats captured. During the study, 24 percent of adult female bats captured were classified as either lactating (n=8), gravid (n=6), or postpartum (n=1). The observed low fecundity is likely due to the cold and wet weather experienced during the study. Information needs for the effective management of bat populations include knowledge of distribution, population status, and habitat requirements. Echolocation monitoring and mist-netting can provide much-needed information that is the first step toward protecting bat habitat.

Rosenberg, D. K., and R. G. Anthony. 1992. Characteristics of northern flying squirrel populations in young second- and old-growth forests in western Oregon. Canadian Journal of Zoology 70:161-166.

Location: Western Oregon.

Habitat: Second-growth and old-growth Douglas-fir forest in the Willamette National Forest on the west slope of the Cascade Mountains.

Keywords: Demographics, density, forest management, succession.

Abstract: We compared density, sex-ratio, body mass, and annual recapture rate of northern flying squirrels (*Glaucomys sabrinus*) populations in second-growth and old-growth Douglas-fir (*Pseudotsuga menziesii*) stands in the Oregon Cascade Range. Densities averaged 2.0 and 2.3 squirrels/ha in second- and old-growth stands, respectively. Although densities varied between years within stands, average densities were similar between years. Body mass and annual recapture rate were similar between stand-age classes, although a higher proportion of females was recaptured in subsequent years in second-growth than in old-growth stands. Similarly there was a higher proportion of females than males in second-growth but not in old-growth stands. Squirrel densities were not correlated with habitat characteristics; we concluded that flying squirrels may be habitat generalists, and not a species associated with old-growth stands, as was previously hypothesized. We suggest that studies be carried out with radiotelemetry to more accurately assess the habitat associations of this species.

Rosenberg, D. K., K. A. Swindle, and R. G. Anthony. Habitat associations of California red-backed voles in young and old-growth forests in western Washington. Northwest Science 68(4): 266-271.

Location: Western Oregon.

Habitat: Douglas-fir, western hemlock stands 30-60 yr and >400 yr.

Keywords: Early seral, habitat associations, old growth, succession.

Abstract: Because of the reduction of old-growth forests in the Pacific Northwest, and the controversy over timber management practices, patterns of animal abundance in young and old-growth forests have gained attention. Results from previous studies on California red-backed voles (*Clethrionomys californicus*), however, have been inconsistent; unmanaged young stands were reported to have similar abundance of California red-backed voles as old-growth stands, while other studies suggested that numbers are higher in older stands. We compared California red-backed vole abundance in five young (30-60 years old) and five old-growth (>400 years old) Douglas-fir (*Pseudotsuga menziesii*) stands in the central Oregon Cascade Range during spring 1988-1991. The average number of red-backed voles captured was consistently higher in old-growth stands ($\bar{x} \pm$ SE, 8.4 ± 1.9) than in young stands (2.0 ± 0.8) during the five years of the study; 80 percent of the voles captured in the five young stands were from one, unmanaged fire-regenerated stand. Our results support hypotheses of lower abundance of California red-backed voles in managed young forests than in unmanaged older forests. Providing components of old-growth forests such as deep organic soil depths, residual large trees and snags, and coarse woody debris in managed young stands will likely increase their potential as suitable habitat for California red-backed voles.

Scrivner, J. H., and H. D. Smith. 1984. Relative abundance of small mammals in four successional stages of spruce fir in Idaho. Northwest Science 58(3):171-176.

Location: Idaho, Pierce Ranger District, Clearwater National Forest.

Habitat: Grand fir; four stand ages (1-10, 11-39, 40-79, 80+ years post-disturbance).

Keywords: Habitat associations, small mammal abundance, successional stages.

Abstract: This paper discusses the relative abundance of four small mammal species in successional stages (1-10, 11-39, 40-79, and 80+ years following disturbance) of spruce-fir forest in Idaho. Species evaluated include *Peromyscus maniculatus*, *Eutamias ruficaudus*, *Zapus princeps*, and *Clethrionomys gapperi*. For the specific study sites we investigated, intraspecific comparisons indicated *P. maniculatus* increased with succession; *E. ruficaudus* abundance varied but was generally most common in mid-successional stages; *Z. princeps* preferred willow-alder thickets within mid-successional stages; and *C. gapperi* was most abundant in the mature forest.

Shepherd, J. F. 1994. Initial response of small mammals to new forestry and overstory removal timber harvests. Master's Thesis, University of Montana, Missoula, Montana. 84 pp.

Location: Western Montana, Swan Valley.

Habitat: Mature Douglas-fir.

Keywords: Habitat selection, new forestry, overstory removal, small mammal abundance, timber management.

Abstract: This study examined the initial response of small mammals to new forestry and overstory removal timber harvest methods as part of a larger biodiversity project. Four sets of experimental plots were located within 13 km of each other in the Swan Valley of western Montana. Each set of plots contained an uncut control and two treatment types: new forestry and overstory removal. Small mammals were trapped on all 12 experimental plots during June and August of the pre- and post-harvest field seasons. Vegetation was sampled on each trapping grid in August of each field season. Analysis of pre-treatment vegetation showed no significant difference among understory or overstory variables. No significant change in vegetative cover or density of small trees was found in the post-treatment season. Density of large trees was significantly different between the controls and treatments in the post-treatment season. Although no significant treatment effect on the abundance of any small mammal species was found, trends in abundance were apparent. The red-tailed chipmunk (*Tamias ruficaudus*) appeared to decline in response to harvest while the yellow-pine chipmunk (*Tamias amoenus*) and red-backed vole (*Clethrionomys gapperi*) increased. Further analysis was conducted to determine habitat associations for the most numerous small mammal species in the pre- and post-harvest seasons. Small mammal trapping in riparian buffers examined the initial response of small mammals to overstory removal timber harvest adjacent to riparian areas. Differences in small mammal abundances for riparian traps rows (A and B) versus upland trap rows (C through E) and harvested versus unharvested plots were statistically tested. Numbers of individuals caught for all species combined and for the red-backed vole (*Clethrionomys gapperi*) were significantly higher than expected in riparian rows of the overstory removal grids and upland rows of the control grids. Distribution of the meadow vole (*Microtus pennsylvanicus*) was not significantly different from random.

Spencer, A. W., and D. Pettus. 1966. Habitat preferences of five sympatric species of long-tailed shrews. Ecology 47(4):677-683.

Location: Larimer county, Colorado.

Habitat: Sedge marsh, subalpine forest (lodgepole pine, spruce, and fir), and clearcut forest at 9,700 feet.

Keywords: Habitat association, population estimates, shrews, clearcutting

Abstract: Long-tailed shrews of five species were captured throughout four years at a single 60-acre site at 9,700 ft elevation in western Larimer County, Colorado. Interspecific differences were significant in the proportions of captures in three main habitats: sedge marsh, subalpine forest, and clearcut forest. All species except one, *Sorex palustris*, were captured in all three types, however. *S. palustris* was taken only adjacent to bodies of water. *Sorex cinereus* and *Sorex vagrans* were captured with the greatest relative frequency in marsh situations. The frequency of captures of the former species in the clearcut habitat was proportionally lower than for the latter species. *Sorex nanus* and *Microsorex hoyi* were taken with high frequency in the forest. *S. nanus* was taken with the greatest frequency of any species in the clearcut area and also at the greatest mean distance from permanent surface water. *M. hoyi* was captured more frequently than any other species at sites intermediate in character between marsh and forest. It was captured much less frequently in the clearcut area and more frequently in the marsh than *S. nanus* but less frequently in the marsh than either *S. cinereus* or *S. vagrans*. Indices of relative abundance of *S. cinereus* and *S. vagrans* synchronously declined sharply in 1963 from high points in 1962 but increased again in 1964. Indices for *S. nanus* and *M. hoyi* remained approximately uniform throughout the four years.

Stoecker, R. E. 1967. A population study of five species of small rodents in the Bridger Mountains of Montana. Master's Thesis, Montana State University, Bozeman, Montana. 32 pp.

Location: Bridger Mountains, southwestern Montana.

Habitat: Grass-forb, sedge and clove communities within a Douglas-fir clearcut at 6100 feet.

Keywords: Habitat association, home range, population estimates.

Abstract: Beginning in June 1966, a one year study of five species of rodents was conducted in the Bridger Mountains of southwestern Montana. Live trapping was performed each month except during winter (December through April). The main objectives were to study the home ranges, population sizes, and habitat preferences of the following species: *Microtus montanus*, *M. pennsylvanicus, Peromyscus maniculatus, Zapus princeps* and *Clethrionomys gapperi*. The vegetation on the 9.6 acre study plot was quantitatively sampled using 1.5 x 3 foot quadrats. Grass-forb, sedge, and clover communities were described.

M. montanus and *M. pennsylvanicus* were lumped in the analysis because they could not be distinguished in the field. Mean home range sizes for 29 males and 37 females were 0.32 and 0.18 acre respectively. A marked population fluctuation was noted, and a peak density of 10.3 *Microtus* per acre was estimated for early August. The breeding season was from July through September. Winter survival was estimated to be 20.6 percent. The overall sex ratio was 1:1, but significantly more females were present in August and significantly more males were present in October and November. The grass-forb community was the preferred habitat.

Mean home range sizes for five male and seven female *Peromyscus* were 0.82 and 0.52 acres, but differences between sexes were not significant. The population remained small with generally from five to eight individuals present. The more xeric areas were the preferred habitats.

The mean home range of eight *Zapus* was 0.40 acres. Estimates of numbers were not made because few recaptures occurred. A total of 55 individuals was captured. The last capture of 1966 occurred on August 18; the earliest capture occurred on May 23, 1967. The possibility of animals moving away from the study plot and returning at a later date was discussed. The more mesic areas were the preferred habitats.

The mean home range of four *Clethrionomys* was 0.19 acre. The largest number of individuals known to be present on the study plot was five during September. Old log piles were the preferred habitats.

Tallmon, D. and L. S. Mills. 1994. Use of logs within home ranges of California red-backed voles on a remnant of forest. Journal of Mammalogy 75(1): 97-101.

Location: Klamath Mountains, Siskiyou National Forest, southwestern Oregon.

Habitat: Old-growth Douglas-fir.

Keywords: Coarse woody debris, home range, logs, microhabitat use, radiotelemetry.

Abstract: We used radiotelemetry to investigate patterns of space use of the California red-backed vole (*Clethrionomys californicus*) on a remnant forest in southwestern Oregon. We radiotracked four voles and mapped the locations of logs of varying decay classes within the home range of each vole. Of the collective locations of voles, 98 percent coincided with downed logs even though logs covered only 7 percent of the areas of estimated home ranges. Furthermore, voles used logs in later stages of decay significantly more often than logs in earlier stages of decay. This high use of decayed logs suggests that decayed logs are a critical component of suitable habitat for voles.

Ure, D. C., and C. Maser. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology 60:3307-3315.

Location: Oregon and Washington.

Habitat: Various coniferous forests.

Keywords: Elevation, hypogeous, food habits, fungi, mycophagy, mycorrhizal.

Abstract: We analyzed stomach contents from two subspecies of *Clethrionomys californicus* and three subspecies of southern red-backed vole from coniferous forests of Oregon and western Washington. Seasonal diets were determined for each subspecies of *C. californicus*. Major foods eaten were the fruiting bodies of hypogeous ectomycorrhizal fungi, predominantly Gastromycetes, and fruiticose lichens, regardless of season. Fungus consumption partially depended on availability. When fungi became scarce, lichens were substituted. Other foods were important only in winter in Cascade Range. *Clethrionomys gapperi* from Washington consumed large quantities of conifer seed and green plant parts in midautumn. These materials were a small part of the diets of Oregon red-backed voles in midautumn, but this may relate to localized small seed crops. Dependence on ectomycorrhizal fungi by western red-backed voles probably accounts for the latter's disappearance from deforested sites.

Walters, B. B. 1991. Small mammals in subalpine old-growth forest and clearcuts. Northwest Science 65(1):27-31.

Location: British Columbia.

Habitat: Old-growth hemlock/fir, clearcut burned, clearcut unburned.

Keywords: Burn, clearcut, old growth, population estimates.

Abstract: This study examined the differences between small mammal populations in a subalpine old-growth forest and adjacent burned and unburned clearcuts. Small mammals were lived trapped, marked, and recaptured weekly during July and August of 1987. Deer mice (*Peromyscus maniculatus*) and chipmunks (*Tamias amoenus*) were most abundant in the two clearcuts; shrews (*Sorex cinereus*) were common in all three habitats; and red-backed voles (*Clethrionomys gapperi*) were common in all but the burned clearcut and the forest edge adjacent to the unburned clearcut. This latter finding may reflect an "edge effect." There were more adult female deer mice and a smaller ratio of juvenile to adult female deer mice in the forest than in the clearcuts. This study suggests that the general effects of clearcutting on small mammals are similar in lowland and subalpine forests, and that edge effects are an important consideration for future research, particularly in old-growth forests.

Worthington, David J. 1991. Abundance, distribution, and sexual segregation of bats in the Pryor Mountains of South Central Montana. Master's Thesis, University of Montana, Missoula, Montana. 40 pp.

Location: Prior Mountains, southcentral Montana.

Habitat: Arid desert, caves, Douglas-fir.

Keywords: Bats, caves, demographics, habitat use, mist netting, roosts, sex ratios.

Abstract: Bat occurrence in the Pryor Mountains of south-central Montana was examined between June and September in 1989 and 1990. A total of 1,319 individuals representing 10 species were captured. Bats were captured at ponds, springs, and at the entrance of five caves. Numbers of bats captured were generally greater at the caves. Capture success was considerably lower at water sources, but a greater diversity of species was noted at these sites. While several of the species captured occurred throughout the area, the spotted bat, *Euderma maculatum*, the pallid bat, *Antrozous pallidus*, and the silver-haired bat, *Lasionycteris noctivagans*, were more restricted in distribution. Two specimens of the spotted bat, *Euderma maculatum*, were captured, representing the first spotted bats captured in Montana since 1949. Spotted bats were observed throughout the eastern portion of the study area. Townsend's Big-eared bat, *Plecotus Townsendii*, was previously known only from winter records in the Pryor Mountains; nine individuals of *Antrozous pallidus* were captured, the first specimens observed since the species was first documented in Montana in 1979. Several of the species of bats found in the Pryor Mountains were captured in numbers significantly different from an expected 1:1 sex ratio. This was especially true at the caves, where males of most species greatly out numbered females, suggesting that males and females may be differentially utilizing habitat. The generally low temperatures of the caves investigated in this study may preclude their summer use by many female bats, especially pregnant or lactating individuals, which require higher roost temperatures to maintain the higher metabolic rate necessary for raising young. Bat activity at the caves, especially Mystery Cave, indicated that these caves provide important summer roosting habitat. Additionally, these caves possess characteristics which may make them important as hibernacula.

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