Nongame Wildlife Research in Subalpine Forests of the Central Rocky Mountains

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Abstract--Subalpine forests of the central Rocky Mountains provide habitat for 145 species of amphibians, reptiles, birds, and mammals. Perhaps because of extreme seasonal climate and the relatively simple structure and composition of subalpine forest, diversity of wildlife is lowest of any forest type in the region. No species are found only in subalpine habitats but some, e.g., southern red-backed vole, reach their maximum abundance there. Research to date has emphasized community structure; much additional work is needed to understand population dynamics and habitat relationships of species that find optimum habitat conditions in subalpine forests.

Subalpine forests of Engelmann spruce, subalpine fir, and lodgepole pine cover about 5 million ha of forest land in Colorado and Wyoming and account for over 90% of sawtimber volume (USDA Forest Service 1980). The climate of the subalpine zone is harsh. Subalpine forests occur at elevations ranging from about 2,700 to 3,600 m where the mean annual temperature is about 2°C. Annual temperature variation is extreme, ranging from -45°C to over 30°C. Annual precipitation varies from 50 to 90 cm, falling primarily as snow from October through May. The frost-free period is very short, usually less than 60 days.

As a result of these harsh conditions, subalpine forests are rather simple in composition and annual productivity is low. Engelmann spruce and subalpine fir are usually codominant although one species may dominate in some stands. At lower elevations and on drier sites, lodgepole pine is often associated with spruce and fir and, on southerly slopes, sometimes occurs in pure stands. Understory cover is usually sparse, consisting primarily of common juniper and grouse whortleberry.

The purposes of this report are to (1) summarize field studies of the occurrence of nongame wildlife species in subalpine forests, (2) compare the fauna of subalpine to other Rocky Mountain forest habitats, (3) compare the fauna of the Rocky Mountains with that of coniferous forests in other regions in North America, (4) briefly summarize the status of our knowledge of habitat associations of subalpine wildlife, and (5) to summarize results of studies documenting the responses of these species to habitat disturbance caused by fire and logging.

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THE SUBALPINE VERTEBRATE COMMUNITY

Diversity of wildlife in subalpine forests is the lowest among habitat types in the central Rocky Mountain region (fig. 1). Hoover and Wills (1984) list 5 amphibian species, no reptiles, 38 mammals, and 76 birds that occur in subalpine forest of Colorado. If lodgepole pine (which is considered a separate habitat type by Hoover and Wills) is included within subalpine, a total of 5 amphibian, 2 reptile, 93 bird, and 45 mammal species occur in the combined habitat types in Colorado (fig. 2). The Wyoming Wildlife Database (Anderson and Patterson 1983) includes 2 amphibians, 4 reptile, 83 bird, and 52 mammal species that occur in subalpine forest of Wyoming.

Not only is the diversity of vertebrates low in subalpine forest compared to other habitat types in the Rocky Mountain region, vertebrate diversity in coniferous forests of the Rockies is low compared to other North American regions. When Wiens (1975) compared numbers of bird species reported in censuses conducted in Rocky Mountain conifer habitats to averages in the northeast, southeast, northern, Sierra Nevada, and northwest coastal forests, he found that Rocky Mountain forests supported an average of 14.0 bird species compared to 14.5-22.6 species in the other regions.

Most of the vertebrate species listed for subalpine habitats also occur in other forest habitats (figure 2, after Hoover and Wills 1984: Appendix A). For example, if one compares the list of species in subalpine habitat to lodgepole pine (fig. 2), most of the species for the combined habitats occur in both. A lesser number occur in lodgepole but not subalpine, and still fewer occur in subalpine but not in lodgepole. Among reptiles and amphibians, species overlap between subalpine and other

habitats (number of species occurring in both habitats divided by the total species occurring in the two habitats) was greatest with aspen and high elevation riparian habitats (71% each) and lowest with ponderosa pine (22%). For both birds and mammals, overlap was greatest with lodgepole pine (76% for each group) and, as was the case for reptiles and amphibians, lowest for ponderosa pine (53% for birds, 44% for mammals). Thus, few species occurring in subalpine habitat are unique to that type.

The overall similarity of wildlife species (percentage of species shared) among Rocky Mountain habitats is shown in figure 3. Subalpine and high elevation riparian habitats are most similar for reptiles and amphibians, followed by aspen, Douglas-fir, and lodgepole pine. These habitats form one related group that is only slightly similar (20%) to the remaining habitats. The overall clustering of habitats for birds and

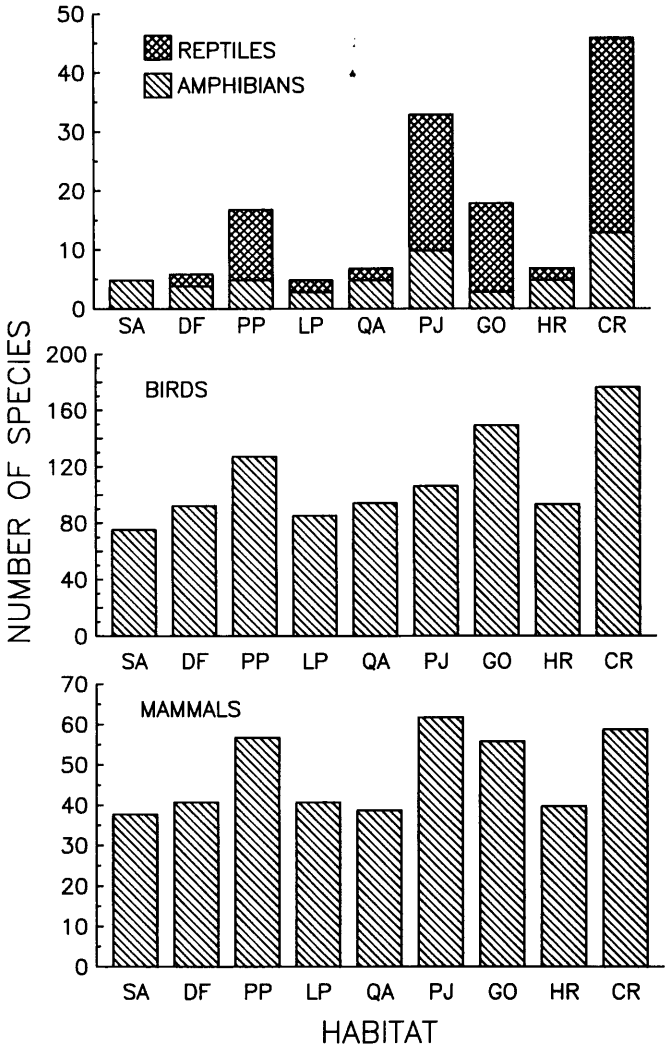

Figure 1.--Number of species of reptiles, amphibians, birds, and mammals in Colorado habitats (SA = subalpine, DF = Douglas-fir, PP = ponderosa pine, LP = lodgepole pine, QA = quaking aspen, PJ = pinyon juniper, GO = Gambel oak, HR = high elevation riparian, CR = cottonwood riparian). Data from Hoover and Wills (1984).

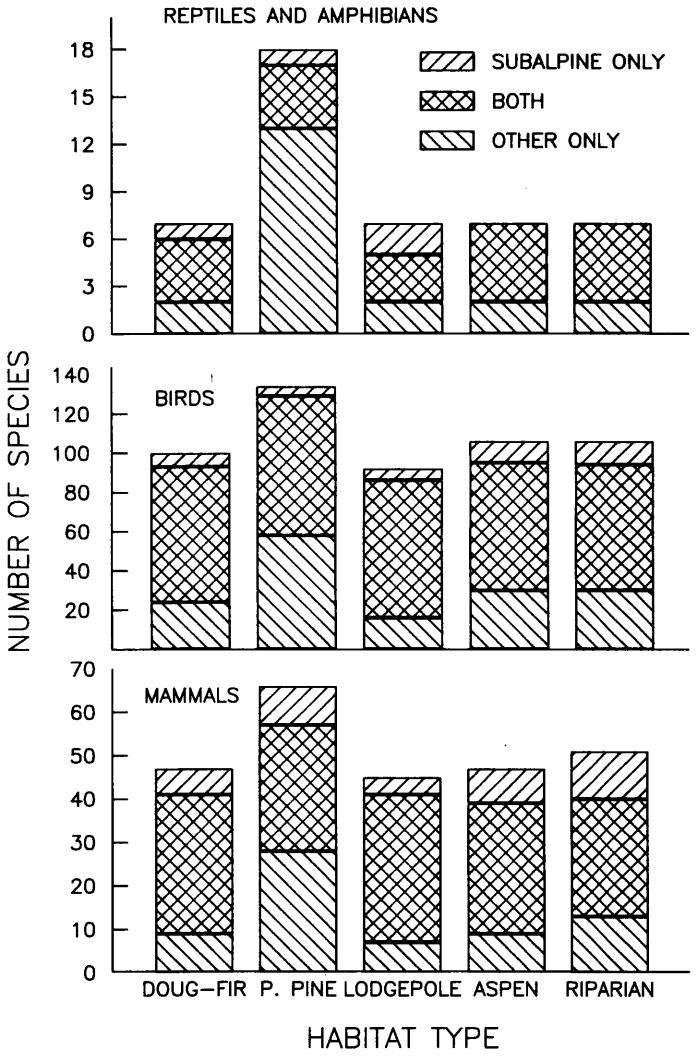

Figure 2.--Comparisons of species composition of subalpine forest with other forest types in Colorado (crosshatching indicates the number of species in common between subalpine and each other habitat type).

mammals follow a similar pattern, except that ponderosa pine is included with the subalpine group for birds. These cluster analyses show that wildlife species are fairly similar between the high elevation conifer, aspen, and riparian habitats and are similar between a lower elevation juniper, oak and cottonwood habitats but that the two groups of habitats share few species.

To better characterize the bird community associated with subalpine habitats, I reviewed all available published census data for the central Rocky Mountain region. This review yielded 19 studies which report occurrence of birds from a total of 54 sites described as subalpine forest. These studies reported 75 bird species, almost half of which were rare, occurring on fewer than 10 percent of the sites (table 1). Fourteen species occurred on 50 percent or more of the sites (table 2). Because these species are widespread among the sites included in this survey, they may be considered most typical of subalpine forest. It is interesting to note that most of

these species are also distributed throughout coniferous forests of North America (table 2). The most narrowly distributed species among those listed are mountain chickadee and Cassin's finch, which occur only in the Sierra Nevada in addition to the Rocky Mountains.

Most of these abundant species feed on insects or seeds in canopy foliage; lesser numbers forage on the ground or are timber drilling or searching. Wiens (1975) compared the distribution of birds among regions based on their foraging position (foliage, ground, timber, air) and found that foliage-feeding species dominated in all North American coniferous forests. Rocky Mountain birds, however, had the highest

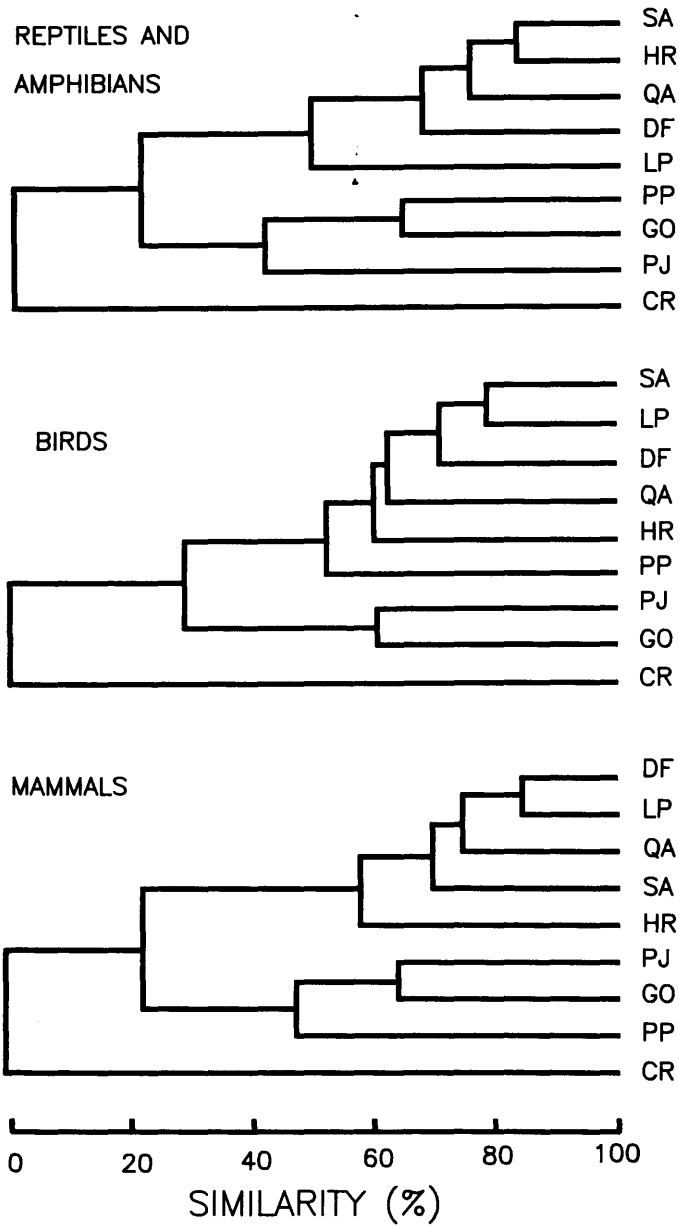

Figure 3.--Overall similarity (percentage of species shared) among Colorado habitat types (see figure 1 for abbreviations). Vertical lines joining groups indicate percent similarity of numbers of the group.

Table 1.--Frequency of occurrence (%) of bird species recorded during census of 54 subalpine forest plots in the central Rocky Mountains.[1]

Species	Percent occurrence among 54 sites
Northern Harrier *(Circus cyaneus)*	2
Sharp-shinned Hawk *(Accipiter striatus)*	6
Cooper's Hawk *(Accipiter cooperii)*	9
Northern Goshhawk *(Accipiter gentilis)*	9
Red-tailed Hawk *(Buteo jamaicensis)*	6
Golden Eagle *(Aquila chrysaetos)*	7
American Kestrel *(Falco sparverius)*	4
Merlin *(Falco columbarius)*	4
Blue Grouse *(Dendragapus obscurus)*	11
Ruffed Grouse *(Bonasa umbellus)*	7
Mourning Dove *(Zenaida macroura)*	20
Great Horned Owl *(Bubo virginianus)*	24
Northern Pygmy-Owl *(Glaucidium gnoma)*	4
Boreal Owl *(Aegolius funereus)*	2
Northern Saw-whet Owl *(Aegolius acadicus)*	2
Common Nighthawk *(Chordeiles minor)*	4
Broad-tailed Hummingbird *(Selasphorus platycercus)*	33
Yellow-bellied Sapsucker *(Sphyrapicus varius)*	19
Williamson's Sapsucker *(Sphyrapicus thyroideus)*	30
Downy Woodpecker *(Picoides pubescens)*	7
Hairy Woodpecker *(Picoides villosus)*	50
Three-toed Woodpecker *(Picoides tridactylus)*	14
Black-backed Woodpecker *(Picoides arcticus)*	4
Northern Flicker *(Colaptes auratus)*	44
Olive-sided Flycatcher *(Contopus borealis)*	30
Western Wood-Pewee *(Contopus sordidulus)*	26
Empidonax spp. *(hammondi or oblerholseri)*	35
Western Flycatcher *(Empidonax difficilis)*	20
Purple Martin *(Progne subis)*	6
Tree Swallow *(Tachycineta bicolor)*	20
Gray Jay *(Perisoreus canadensis)*	56
Steller's Jay *(Cyanocitta stelleri)*	15
Clark's Nutcracker *(Nucifraga columbiana)*	39
Black-billed Magpie *(Pica pica)*	6
American Crow *(Corvus brachyrhyncos)*	6
Common Raven *(Corvus corax)*	6
Black-capped Chickadee *(Parus atricapillus)*	19
Mountain Chickadee *(Parus gambeli)*	93
Red-breasted Nuthatch *(Sitta canadensis)*	65
White-breasted Nuthatch *(Sitta carolinensis)*	6
Brown Creeper *(Certhia americana)*	46
Rock Wren *(Salpinctes obsoletus)*	4
House Wren *(Troglodytes aedon)*	19
American Dipper *(Cinclus mexicanus)*	2
Golden-crowned Kinglet *(Regulus satrapa)*	54
Rudy-crowned Kinglet *(Regulus calendula)*	81
Mountain Bluebird *(Sialia currucoides)*	13

(continued)

Table 1.--(continued).

Species	Percent occurrence among 54 sites
Townsend's Solitaire *(Myadestes townsendi)*	30
Swainson's Thrush *(Catharus ustulatus)*	31
Hermit Thrush *(Catharua guttatus)*	74
American Robin *(Turdus migratorius)*	83
Cedar Waxwing *(Bombycilla cedrorum)*	2
Warbling Vireo *(Vireo gilvus)*	24
Yellow Warbler *(Dendroica petechia)*	6
Yellow-rumped Warbler *(Dendroica coronata)*	91
Ovenbird *(Seiurus aurocapillus)*	2
MacGillivray's Warbler *(Oporornis tolmiei)*	9
Wilson's Warbler *(Wilsonia pusilla)*	6
Western Tanager *(Piranga ludoviciana)*	46
Black-headed Grosbeak *(Pheucticus melanocephalus)*	6
Lazuli Bunting *(Passerina amoena)*	7
Green-tailed Towhee *(Pipilio chorurus)*	2
Chipping Sparrow *(Spizella passerina)*	52
Vesper Sparrow *(Pooecetes gramineus)*	2
Song Sparrow *(Melospiza melodia)*	7
Lincoln's Sparrow *(Melospiza lincolnii)*	22
White-crowned Sparrow *(Zonotrichia leucophrys)*	20
Dark-eyed Junco *(Junco hyemalis)*	96
Brown-headed Cowbird *(Molothrus ater)*	9
Pine Grosbeak *(Pinicola enucleator)*	57
Cassin's Finch *(Carpodacus cassinii)*	59
Red Crossbill *(Loxia curvirostra)*	31
White-winged Crossbill *(Loxia leucoptera)*	4
Pine Siskin *(Carduelis pinus)*	87
Evening Grosbeak *(Coccothraustes vespertinus)*	6

[1]*Sources included Snyder 1950 (2 sites), Thatcher 1956, Salt 1957 (3 sites), Webster 1967, Burr 1969, Kingery 1970, 1971, 1973, Winn 1976 (8 sites), Young 1977 (8 sites), Roppe and Hein 1978, Thompson 1978 (4 sites), Austin and Perry 1979 (2 sites), Harvey and Weaver 1979 (2 sites), Taylor and Barmore 1980 (3 sites), Smith and MacMahon 1981 (2 sites), Scott et al. 1982 (2 sites), Raphael (this symposium, 3 sites), Keller 1987 (10 sites).*

percentage (28%) of ground foraging birds and a lower percentage of foliage feeding birds (53%) compared with percentages of total density in other regions.

Total density of birds is low in Rocky Mountain coniferous forests compared with other regions (fig. 4). Wiens (1975) reported an average of 736 birds/100 ha (s.d. = 575) for all conifer habitats in the Rocky Mountain region. Among those studies reporting total density estimates (as summarized in table 1), I calculated a mean of 577 birds/100 ha (s.d. = 472, n = 31) which is lower than averages of all but the northern region (fig. 4).

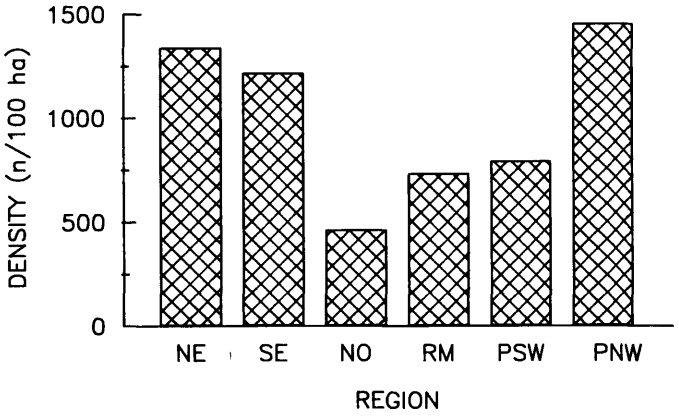

Figure 4.--Comparisons of abundance of birds among conifer forest regions in North America (NE = Northeast, SE = Southeast, NO = Northern, RM = Rocky Mountain, PSW = Pacific Southwest, PNW = Pacific Northwest), after Wiens (1975).

Biomass (total weight of all birds) averages 188 g/ha for all conifer forest types in the Rocky Mountain region (Weins 1975). For subalpine forests, I calculate a similar average of 187 g/ha based on data cited in table 1. Salt (1957) compared bird biomass in several habitat types and separated total biomass into that contributed by herbivores and carnivores (fig. 5). Biomass was much lower in subalpine forest types than in riparian, meadow, and aspen types, primarily because of the greater contribution of carnivores in the latter types. One possible explanation of this pattern is that insect biomass (primarily prey of carnivores) is greater in these habitats than in subalpine forest. In support of this argument, Schimpf and MacMahon (1985) found that insect density, diversity, and mean body size were all at least twice as great in aspen compared to subalpine forest.

Nongame mammals have received little study compared to efforts on birds. I found 11 studies enumerating small mammal faunas in subalpine forests of the Rocky Mountains (table 3). Altogether, these studies list 24 mammal species, of which only

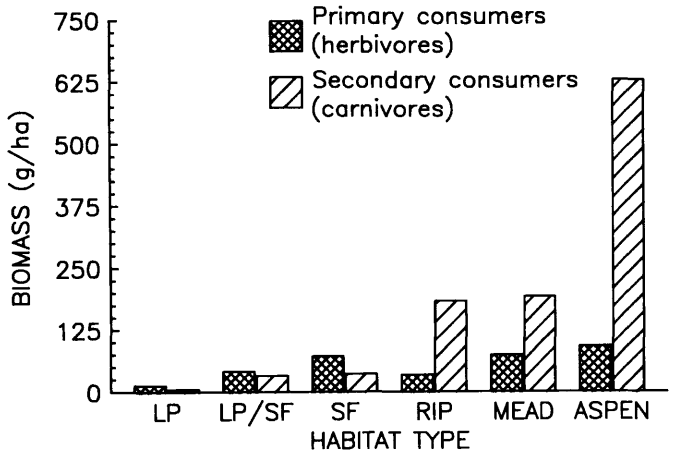

Figure 5.--Biomass of birds among habitat types in Wyoming (LP = lodgepole pine, LP/SF = lodgepole and spruce-fir, SF = spruce-fir, RIP = riparian, MEAD = meadow, after Salt (1957).

Table 2.-- The 14 most commonly reported bird species from subalpine sites (n = 54) in the central Rocky Mountains.[1]

Species	Frequency	Foraging Guild	Distribution[2] NE	SE	NO	SN	PN
Dark-eyed Junco	96	ground-seed	X	X	X	X	X
Mountain Chickadee	93	foliage-insect	X				
Yellow-rumped Warbler	91	foliage-insect	X	X	X	X	
Pine Siskin	87	foliage-seed	X	X	X	X	X
American Robin	83	ground-insect	X	X	X	X	X
Ruby-crowned Kinglet	81	foliage-insect	X	X	X	X	
Hermit Thrush	74	ground-insect	X	X	X	X	X
Red-breasted Nuthatch	65	timber-searching	X	X	X	X	X
Cassin's Finch	59	ground-seed	X				
Pine Grosbeak	57	foliage-seed	X	X	X		
Gray Jay	56	foliage-seed	X	X	X		
Golden-crowned Kinglet	54	foliage-insect	X	X	X	X	X
Chipping Sparrow	52	ground-insect	X	X	X	X	X
Hairy Woodpecker	50	timber-drilling	X	X	X	X	X

[1]*See table 1 for citations.*

[2]*NE = northeast, SE = southeast, NO = northern, SN = Sierra Nevada, PN = Pacific northwest (after Wiens 1975).*

Table 3.--Frequency of occurrence of small mammal species among 29 sites in subalpine forests of the central Rocky Mountains.[1]

Species[2]	Frequency (%)	Species[2]	Frequency (%)
Unidentified Shrew (*Sorex* spp.)	31	Red Squirrel *(Tamiasciurus hudsonicus)*	48
Masked Shrew *(Sorex cinereus)*	14	Northern Flying Squirrel *(Glaucomys sabrinus)*	41
Dusky Shrew *(Sorex monticolus)*	14	Northern Pocket Gopher *(Thomomys talpoides)*	10
Water Shrew *(Sorex palustris)*	7	Deer Mouse *(Peromyscus maniculatus)*	93
Nuttall's Cottontail *(Syvilagus nuttalli)*	7	Southern Red-backed Vole *(Clethrionomys gapperi)*	86
Snowshoe Hare *(Lepus americana)*	34	Heather Vole *(Phenacomys intermedius)*	14
Least Chipmunk *(Tamias minimus)*	28	Meadow Vole *(Microtus pennsylvanicus)*	3
Colorado Chipmunk *(Tamias quadrivittatus)*	3	Montane Vole *(Microtus montanus)*	21
Red-tailed Chipmunk *(Tamias ruficaudus)*	17	Long-tailed Vole *(Microtus longicaudus)*	17
Uinta Chipmunk *(Tamias umbrinus)*	45	Western Jumping Mouse *(Zapus princeps)*	45
Columbian Ground Squirrel *(Spermophilus columbianus)*	3	Porcupine *(Erithizon dorsatum)*	7
Golden-mantled Ground Squirrel *(Spermophilus lateralis)*	28	Ermine *(Mustela erminea)*	10
		Long-tailed Weasel *(Mustela frennata)*	21

[1]*Williams 1955 (2 sites), Negus and Findley 1959 (2 sites), Brown 1967a,b (2 sites), Winn 1976 (8 sites), Austin and Urness 1977 (2 sites), Anderson et al. 1980 (2 sites), Ramirez and Hornocker 1981 (2 sites), Scrivner and Smith 1984 (4 sites), Palmer 1986 (2 sites), Raphael (these proceedings, 3 sites).*

[2]*Names follow Jones et al. 1982.*

2 (deer mouse and southern red-backed vole) occurred on over half of the 29 sites sampled; 17 species occurred on less than one-third of the sites. The deer mouse is distributed throughout North America in nearly every habitat, forested and nonforested. The southern red-backed vole occurs in forests of Canada, the Rocky Mountains, and the northestern states. In many of the studies listed in table 3, this species was the most abundant small mammal and seems to find subalpine forest as its optimum habitat (e.g., fig. 6).

Whereas fewer species of small mammals are sampled in subalpine forest compared with birds, biomass of mammals is much higher. Vaughan (1984) estimated biomass of mammals in subalpine meadows from 3,171 to 3,537 g/ha in a three-year study; Anderson et al. (1980) estimated values from 2,228 g/ha on a spruce site to 3,593 g/ha on a fir site. These values, though undoubtedly subject to large error due to difficulties estimating small mammal density, are an order of magnitude greater than values for birds (which averaged only 187 g/ha, and ranged from 69 to 611 g/ha). In contrast to birds, most of the biomass of small mammals (67%) is contributed by herbivorous species (Vaughan 1984).

HABITAT ASSOCIATIONS

General Relationships

Compared to forests in other regions in North America, subalpine forests of the central Rocky Mountain area have received little study regarding habitat relationships of nongame wildlife. Hoover and Wills (1984) summarize general principles and report abundance of management indicator species in seral stages of major forest habitat types (ecosystems) in Colorado. Similar tabulations are available for Wyoming (Bernard and Brown 1978, Findholt et al. 1981, Anderson and Patterson 1983, Baxter and Stone 1985) but these are based more on professional judgement and general ecology than on results of local research.

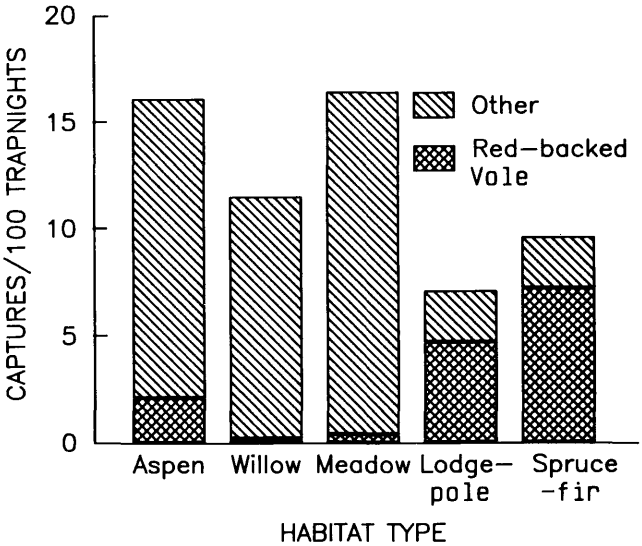

Figure 6.--Abundance of southern red-backed voles and other small mammal species in Rocky Mountain habitats (Brown 1967a).

In one of the few bird community studies, Young (1977) examined bird diversity (numbers of breeding species) in relation to 14 structural features of subalpine forest. She found that diversity of tree diameters was the single best predictor of bird diversity ($R^2 = 0.73$); as diameter diversity increased, bird diversity increased. Winn (1976) found, in contrast, that plant species diversity was the best predictor of bird species diversity.

As summarized by Scott et al. (1980), cavity-nesting birds comprised about 25% of the total breeding density of birds in subalpine forest (range = 13-40%). Thus, the abundance and characteristics of snags is an important forest attribute. Scott et al. (1978, 1980) surveyed snags at the Fraser Experimental Forest in Colorado and found that lodgepole pine, Engelmann spruce and subalpine fir snags greater than 12 inches dbh were used for nesting at rates greater than expected from their availability, and that broken-topped snags of all three species also received the greatest use. Overall, only 3% of 1,722 snags sampled had nest cavities, but 33% of broken-topped snags > 12 inches d.b.h. had cavities.

Habitat associations of small mammals seem to have received more study, but detailed analyses of mammal communities in relation to habitat structure are lacking. The following examples illustrate typical studies from subalpine forests. Spencer and Pettus (1966) examined habitat associations of five shrew species. The presence of surface water was an important habitat feature. Dusky and dwarf shrews tolerated the most xeric conditions, masked and pygmy shrews were intermediate, and the water shrew was found only in close proximity to water. Brown (1967b) found a much greater abundance of masked shrews in boggy habitats, whereas dusky shrews were predominant in upland sites and pygmy shrews were associated with rock outcrops. The importance of moisture was also noted by Armstrong (1977).

Brown (1967a) related abundance of mice to proximity of water and cover density. Jumping mice and long-tailed voles were more abundant near water; montane voles, southern red-backed voles, and deer mice were more abundant on sites further from water (> 175 m away). Jumping mice, long-tailed voles, and montane voles were most abundant in dense understory cover; red-backed voles and deer mice were about equally abundant in all cover classes. Sleeper (1979) examined small mammal population fluctuation in relation to snowpack over a 6-year period, and found significant and negative correlations between summer population numbers and snowpack the previous winter for five mammal species. Deep snowpack appeared to depress population numbers. In a detailed study of the winter ecology of the southern red-backed vole, Merritt (1976, 1985) and Merritt and Merritt (1978) found that autumn freeze and spring thaw were periods of greatest hardship and poorest survival. Telleen (1978) compared the distribution of least and Uinta chipmunks at Rocky Mountain National Park, and reported that the Uinta

chipmunk preferred closed canopy forest with an open understory, whereas the least chipmunk favored open canopy and closed understory.

Studies of habitat associations of reptiles and amphibians are virtually nonexistent in subalpine forest, primarily because reptiles and amphibians are virtually nonexistent. Baxter and Stone (1985) have summarized habitat associations of subalpine species in Wyoming; Hammerson and Langlois (1981) do so for Colorado, but their habitat descriptions are limited to lists of habitat types in which each species is known to occur. Haynes and Aird (1981), in one of the more detailed analyses of habitat requirements, found that the wood frog breeds primarily in small (< 0.25 ha) natural ponds with emergent vegetation along a shallow north edge.

Responses to Disturbance

Fire

Fire-induced secondary succession in subalpine forest systems is accompanied by marked changes in bird and small mammal populations (Taylor 1971, Davis 1976, Roppe and Hein 1978, Ramsden and Lyon 1979, Taylor and Barmore 1980). In general, these studies show that biomass of birds and small mammals is greater in burned compared with unburned forest. Overall, biomass of birds is highest within the first 10 years following fire, then decreases during the intermediate period from 50-100 years following fire when, in the absence of further disturbance, stands are often overstocked and stagnated (fig. 7). Biomass increases thereafter to prefire levels. The general pattern varies, however, among birds in various feeding categories. Ground-foraging and timber-drilling birds are more abundant in burned forest, but seed- and insect-eating birds associated with the overstory canopy are more abundant in unburned forest (Taylor and Barmore 1980).

Similar patterns are also found among small mammals. Roppe and Hein (1978) estimated a biomass of small mammals of 1,020 g/ha on an 8 year-old burn compared to 764 g/ha

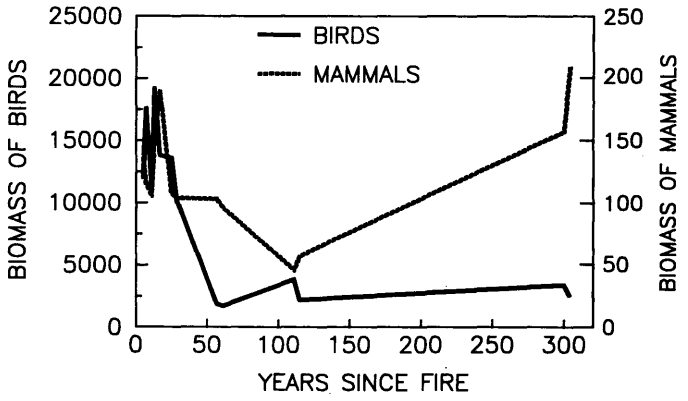

Figure 7.--Biomass (g/40) of birds and small mammals on various burned study areas (Taylor 1971).

in unburned forest. Red squirrels and showshoe hares, not counted in these totals, were absent in the burn. Shrews, golden-mantled ground squirrel, deer mouse, heather vole, and long-tailed vole were all more abundant on the burned plot, whereas southern red-backed vole was rare on the burn and abundant in the unburned forest. Chipmunks were equally abundant in both burned and unburned habitats. Taylor (1971) found that small mammal biomass, like that of birds, was lowest during the intermediate period of postfire succession (fig. 7).

Timber Harvest

Birds seem to respond to timber harvest in patterns similar to their responses to fire. Austin and Perry (1979) found much higher densities of birds in 25- and 15-year-old clearcuts (302 and 538 birds/100 acres, respectively) than in mature forest (134 birds/100 acres). Most of these differences were due to higher abundance of American robin, Cassin's finch, pine siskin, and chipping sparrow on the clearcuts. These are ground-foraging seed and insect eaters that are favored by opening the overstory canopy. In this study, only the hermit thrush (a ground-insect forger that nests in closed canopy format) and ruby-crowned kinglet (a canopy-insect forager) were more abundant in the mature forest.

Scott et al. (1982) found no significant short-term change in total numbers of birds during 2 years immediately after 36% of a 40-ha timber stand was harvested in 12 small clearcuts on the Fraser Experimental Forest. They did find significant declines in abundance of golden-crowned and ruby-crowned kinglets; no birds increased significantly, but the Lincoln's and song sparrow were observed on the harvested drainages following treatment but had not been observed prior to treatment.

The influences of slash disposal and other site preparation practices on the post-harvest suitability of stands were studied by Davis (1976). He found that increased logging residue, standing dead timber, and understory plant diversity all led to higher abundance of birds on clearcuts. Keller (1987) compared bird abundance in subalpine forest fragmented by recent stripcuts or small patchcuts and compared results to unharvested controls. She identified 6 species that were less abundant in timber adjacent to harvest in at least 1 year during her 2-year study, 4 that were more abundant, and 3 that showed no change. She concluded that brown creeper and red-breasted nuthatch (bark foraging species) were most sensitive to nearby harvest through reduction in their total foraging habitat area.

Studies of small mammal populations following harvest show variable results. Several studies report a net decrease in total abundance on clearcut sites compared to uncut sites (Porter 1959, Spencer and Pettus 1966, Austin and Urness 1977, Scrivner and Smith 1984), two studies report a net increase (Davis 1976, Ramirez and Hornocker 1981), and two studies showed no net change Campbell and Clark 1980, Scott

et al. 1982). The response of individual species was more consistent. Southern red-backed voles, for example, are consistently reported as much lower or absent in clearcuts, whereas deer mice, vagrant shrews, and least chipmunks are consistently more abundant in clearcuts. As reported among birds, site preparation and the nature of residual vegetation following logging are important in determining the suitability of post-harvest habitat for small mammals. Several studies (e.g., Davis 1976, Campbell and Clark 1980, Ramirez and Hornocker 1981) found a greater abundance of small mammals on clearcut sites with greater volume of slash or with thicker residual understory vegetation.

CONCLUSIONS

Studies of nongame wildlife in the central Rocky Mountains reveal that subalpine forests support low numbers of species and low population sizes of most species relative to other habitat types in the Rockies, and relative to other coniferous forest systems in North America. This rather depauperate fauna may be due to climatic extremes typical of the subalpine zone and the resulting low productivity of the forest. The few species that are abundant in subalpine forests tend to be widespread in distribution and are abundant in other forest types as well. Several species, including birds listed in table 2 and mammals such as the southern red-backed vole and marten, reach their peak in subalpine forest. Because of the extreme climate and the variability of snowfall and other weather factors from year to year, annual variation of population sizes of subalpine wildlife is great, suggesting that those species that winter in subalpine habitats may more often be limited by abiotic factors than by habitat.

Habitat associations of subalpine wildlife have received some study, but a great deal more research is needed. In particular, I found no studies of habitat associations of bats, a group that includes 14 species in Rocky Mountain forests but about which very little is known. There have been no long-term studies of nongame populations in relation to vegetation succession following fire or logging. Detailed quantitative studies of forest structure in relation to vertebrate community structure are lacking although some studies are underway. Much better information is needed on the distribution and occurrence of nongame wildlife species in the National Forests and Parks. The recent study by Newmark (1987), purporting to show evidence of losses of up to 43% of the original species among 14 National Parks in western North America, highlights the need to conduct a well-organized survey or inventory of the status of vertebrate species in our managed lands.

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