WILDLIFE

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Aspen forests provide important habitat for many species of wildlife (Gullion 1977b), especially in the West (see the appendix to this chapter). In the coniferous forests of the interior West, aspen groves may be the only source of abundant forage; in the grasslands they may be the sole source of cover. A primary value of the aspen ecosystem in the West during the past century has been production of forage for both wildlife and domestic livestock (see the FORAGE chapter).

This chapter examines the values of the aspen ecosystem to wildlife, specifically birds and mammals. The ANIMAL IMPACTS chapter discusses the interaction of the aspen plant community and animals from the opposite point of view—the effects of animals on the plant community.

Most of the aspen in the Rocky Mountain states is in national forests. Table 1 provides population estimates for selected wildlife species that use aspen as habitat on these forests.[1] Although aspen is not essential to all these animals, it may be quite important to some populations.

Together, Colorado and Utah have nearly 4 million acres (1,575,000 ha) of aspen forest. These stands are extensive and form a major habitat component for many species. In Montana, Idaho, and Wyoming, there are about 1 million acres (470,000 ha) of aspen. The aspen communities in these states often are interspersed with much more extensive coniferous forest lands or, in some cases, with grasslands. This distribution pattern makes these aspen very valuable for some wildlife species. The three drier states of New Mexico, Arizona, and Nevada have less than 500,000 acres (200,000 ha) of aspen. However, they also have sizable wildlife populations on their national forests.

[1] *U.S. Department of Agriculture, Forest Service. 1980. Wildlife and fisheries report 1980: Population estimates, hunter harvest, habitat accomplishments, and sportsman use. USDA Forest Service, Wildlife and Fisheries Staff, Washington, D.C.*

BIRDS

The diversity and species richness of birds in the aspen ecosystem in western North America (see the chapter appendix) reflects the variation in this ecosystem over a wide geographic area, as well as the variety of understory types, elevational zones, and associated tree species within the aspen type locally. Some of the birds listed, such as the sandhill crane, are a part of the ecosystem locally; others, such as the western wood pewee, are a part of almost the entire aspen ecosystem throughout the West. Among the game species, there are six species of ducks, two species of forest grouse (blue and ruffed), two species of pigeons (band-tailed and mourning dove), the sharp-tailed grouse, and the wild turkey that utilize aspen habitats.

Both pure and mixed aspen stands are included in the aspen ecosystem; if aspen comprises more than 50% of the overstory, a stand is considered to be part of the aspen forest type. Pure aspen forests, some with and some without shrub understories, and aspen-conifer mixed forests, some with an understory of young conifers, and others with conifers in the overstory, provide markedly different habitats for wildlife, especially

Table 1.—Estimated wildlife populations on national forests in eight western states.[1]

Species	Colorado	Utah	Idaho	Wyoming	Montana	New Mexico	Arizona	Nevada
Mule deer	208,500	170,900	146,000	81,000	106,200	78,600	56,800	61,500
Whitetail deer	200	0	28,100	9,700	47,400	3,100	21,200	0
Elk	104,700	15,100	55,800	53,600	55,200	10,000	11,000	500
Moose	50	950	3,800	7,150	4,650	0	0	0
Bighorn sheep	3,700	50	2,800	4,450	2,950	650	200	300
Bison	0	0	0	240	30	0	120	0
Black bear	5,900	500	16,450	2,500	12,250	2,450	1,850	50
Mountain lion	700	650	1,600	150	900	800	1,300	300
Turkey	3,500	300	800	2,800	2,400	24,900	11,500	200
Total area in aspen type in entire state:								
× 1,000 acres	2,629	1,250	544	427	190	378	89	20
(× 1,000 ha)	(1,064)	(506)	(220)	(173)	(77)	(153)	(36)	(8)

[1] *U.S. Department of Agriculture, Forest Service. 1980. Wildlife and fisheries report 1980: Population estimates, hunter harvest, habitat accomplishments, and sportsman use. USDA Forest Service, Wildlife and Fisheries Staff, Washington, D.C.*

birds. Species diversity probably is greatest in the aspen-conifer mixes, because of the diversity of niches there.

Species such as evening grosbeak, long-eared owl, Clark's nutcracker, western tanager, goshawk, pileated woodpecker, gray jay, Wilson's warbler, kinglets, and the red crossbill are more a part of the conifers than of the aspen. Behle and Perry (1975) listed about 60 species of birds found in the "aspen woodland" type (the pure aspen forest type) in Utah. They also listed species found in the spruce-fir type. Eight species in their spruce-fir list were not found in the "aspen woodland;" 12 species in the "aspen woodland" list were not found in the spruce-fir.

Many bird species in the aspen ecosystem do not breed there. This is especially true during spring and fall migration. For example, of the 21 to 26 species found in a 10-acre (4-ha) Utah aspen stand during each of four summers, only 12 to 19 of them nested in the area (DeByle 1981). Similarly, Smith and MacMahon (1981) listed 71 total species, with 43 of them breeding in a northern Utah meadow-aspen-fir-spruce sere. Winternitz (1976) found similar ratios in Colorado's Front Range. Of the 24 species Smith and MacMahon (1981) found breeding in the aspen type, only 5 of them were year-round residents—the ruffed grouse, hairy woodpecker, mountain chickadee, red-breasted nuthatch, and pine siskin.

Small Birds

Most of the bird species listed in the appendix are classified commonly as songbirds. This category includes all passerine bird species plus other insectivores, granivores, and nectivores that do not fit elsewhere. As individual species, they are too numerous to discuss. Instead, they are grouped, depending on where they nest or upon where and on what they feed. Flack (1976) categorized these birds into nesting guilds: canopy, shrubs, holes, and ground. Canopy nesters, shrub or understory nesters, and ground nesters are discussed in this section. The hole or cavity nesters are discussed separately because of their importance in the forested situation and because of the profound and lasting effect forest cutting or management has on their habitat.

Canopy nesters include the pewee, robin, vireos, yellow-rumped warbler, western tanager, Cassin's finch, and least flycatcher (Flack 1976). Trees are essential for their nesting habitat. Many canopy nesters prefer to feed in the open; these species commonly concentrate on forest edges. Those species that both feed and nest in the forest are distributed throughout the stands.

Shrub nesting bird species include the *Empidonax* flycatchers; rose-breasted and black-headed grosbeaks; chipping, clay-colored, and song sparrows; yellow and MacGillivray's warblers; lazuli bunting; rufous-sided and green-tailed towhees, black-billed cuckoo; and

Figure 1.—Several bird species nest on the ground beneath the aspen canopy. An example is this dark-eyed junco nest beneath the herbaceous understory of a pure aspen stand in Wyoming.

others. Some birds, such as hummingbirds, nest in canopies of both trees and shrubs.

A mature aspen forest with an herbaceous understory probably has few or no shrub nesting bird species, whereas one with an abundant tall shrub understory may have many shrub nesters (Flack 1976). When the mature aspen forest is clearcut, understory plant production increases and thousands of aspen suckers develop (Bartos and Mueggler 1982). This temporarily destroys the nesting habitat for the canopy nesters but improves it immensely for the shrub nesters. A mixed aspen-conifer forest will lose understory as the conifers mature and dominate the site; this reduction in understory as succession proceeds will reduce habitat for shrub nesting birds.

The ground nesting species include the hermit thrush, Townsend's solitaire, junco (fig. 1), white-crowned and Lincoln's sparrows, veery, ovenbird, nighthawk, and the Connecticut and mourning warblers. This group of species often depends on the aspen forest for feeding habitat and on the understory plants for protective cover around their nests. The ground nesters are very susceptible to habitat alteration and trampling by grazing animals. Flack (1976) found that the number of birds nesting or feeding on the ground decreased as litter cover on the forest floor increased.

Birds also can be grouped into feeding guilds—ground-insect, ground-seed, foliage-insect, air-perching, and air-soaring guilds. Each species can be placed in a combined nesting and feeding guild. As examples, the tree swallow is a cavity nester—air-soaring insectivorous species, the warbling vireo is a canopy nester—foliage-insect feeder, the junco is a ground nester—ground-seed eater, and the yellow-rumped warbler is a canopy nester—foliage-insect feeder.

Salt (1957) found the aspen type on a moist site, near Jackson, Wyo., had at least three times the bird biomass of any of the six vegetation types he inventoried. Although this may be a bit extreme, it illustrates the value of aspen for bird habitat. In his sample, more than 85% of this biomass was made up of secondary con-

sumers, mostly insectivorous birds. In the coniferous forest types sampled, there were more primary consumers and fewer bird species.

Aspen growing on dry sites have fewer species and numbers of birds than aspen on wet sites (Salt 1957, Winternitz 1980). Winternitz (1980) found 1–1.5 breeding pairs per acre (3–4 per ha) on a dry site, 2.5–3 per acre (6-8 per ha) on a moist site, and 4 pairs per acre (10 per ha) where there was standing water. Species richness increased proportionately. Not only the wetness of an aspen site, but the stability of that moisture supply also is important to the avian community. During a drought year, Smith (1982) recorded the greatest bird population decline in the aspen community of the meadow-aspen-fir-spruce sere in northern Utah. Nectivorous hummingbirds disappeared, and insectivores declined markedly. He and Winternitz (1980) both emphasized the importance of insect populations as a food resource for birds in the aspen type. Drought reduced this food base.

In an extensive survey of birds inhabiting aspen forests in the West, Flack (1976) found that species richness and bird populations both declined as tree densities increased or average tree diameters decreased. Similarly, in Utah, Young (1973) censused 20 breeding species with a density of 6 pairs per acre (15 per ha) in an open, mature aspen stand, but only 14 species with 3 pairs per acre (7 per ha) in a dense, brushy stand of small trees.

The parkland aspen habitat of north-central Montana and Canada has a different bird community than the montane aspen type of the Rocky Mountains (Flack 1976). Many of the parkland species are typically eastern, such as the eastern kingbird, gray catbird, and black-billed cuckoo. The mix of bird species was greater in the parklands than in the mountane environments to the south or in the aspen stands of the boreal forest farther north.

Cavity Nesters

Cavity nesting bird species are an important part of the aspen forests. Winternitz (1980) found 38% of the breeding species in Colorado aspen forests were cavity nesters; Scott et al. (1980) stated that a range of 17% to 60% of the birds were cavity nesters in aspen stands over a variety of sites.

Some 85 species of birds in North America use tree cavities for nesting; most of these are insectivorous (Scott et al. 1977). About 34 of these species nest in the cavities of aspen in the West. They include the waterfowl listed in the chapter appendix; the American kestrel and merlin; the flammulated, western screech, northern pygmy, and northern saw-whet owls; all of the sapsuckers and woodpeckers in the chapter appendix; the western and great crested flycatchers; the purple martin; the tree and violet-green swallows; all of the chickadees and nuthatches listed in the chapter appendix; the brown creeper; the house wren; the western and mountain bluebirds; and the starling (Harrison 1979, Scott et al. 1977).

Figure 2.—The northern flicker is an important cavity builder in the aspen forest. It provides nest sites for itself and for the many secondary cavity nesting species that may follow. (Photo by Virgil Scott)

There is an abundance of cavity-bearing trees in most aspen forests in the West. Natural thinning proceeds as the typical aspen stand grows and matures. Trees of all sizes may be killed by competition and decay. Death and decay of trees or parts of trees permit excavation of many cavities. As trees grow and mature in a stand, opportunity for cavity nesters improves. Decay at points of injury on large trees make good cavity sites. Commonly, 6% to 20% of the standing trees in mature and overmature aspen stands are dead.[2] However, once dead, an aspen snag is unlikely to stand for more than a few years.

Aspen is very susceptible to heart rot (see the DISEASES chapter). In mature aspen stands, many of the trees that otherwise appear healthy are infested with decay fungi, especially *Fomes igniarius*. The punky interiors of these trees are readily excavated by woodpeckers and are used for nesting by them and other cavity nesting species that may follow. These live trees may stand for many years after initial decay permits cavity excavation. The number of holes drilled in the large infected trees indicates that birds prefer them for nesting (Scott et al. 1980, Winternitz 1980). Crockett and Hadow (1975) and Kilham (1971) stated that sapsuckers were attracted to trees infected by *Fomes*.

By definition, the primary cavity nesters excavate their own cavities. Only the woodpeckers and sapsuckers consistently excavate cavities, usually new ones each year, and often more than they need. Thus, they provide cavities for the secondary cavity nesting birds. Chickadees and nuthatches can excavate their own cavities in soft wood (Scott et al. 1980); other species

[2]*Unpublished data on file at the USDA Forest Service, Intermountain Forest and Range Experiment Station's Forestry Sciences Laboratory, Logan, Utah.*

(owls, swallows, etc.) require available cavities for their nesting sites. Among the primary cavity nesters, the sapsuckers and the hairy and downy woodpeckers prefer aspen trees. Others, such as the flicker, are not as discriminating.

Scott et al. (1980) indicated the importance of the flicker as a cavity nester (fig. 2). Because it is the largest woodpecker in much of the Rocky Mountains, it provides nesting sites in a variety of tree species for many of the larger secondary cavity users. In the mixed aspen-conifer forest, the aspen component probably is essential habitat for some of the cavity nesting birds. As the forest succeeds to spruce and fir, or to pure spruce, which is too hard for most primary cavity nesters, the number of cavity dwellers could be expected to decline (Smith 1980).

Most cavity nesters are insectivorous and are considered to be mostly beneficial to human interests (Thomas 1979). (See the ANIMAL IMPACTS chapter for discussion of negative impacts of cavity construction and sapsucker feeding.) Therefore, guidelines have been developed for snag management in some of the conifer types to retain cavity nesting habitat. Although similar formal guidelines have not been written for aspen, very little modification of current management practices is needed to maximize this habitat. Little, if any, of the aspen forest is harvested until it is mature to overmature; and then, most harvesting is in the form of small (2.5- to 12-acre (1- to 5-ha)) clearcuts. This preserves natural cavity nesting habitat until the stand is overmature. Clearcutting small patches of aspen does more to enhance edge for the birds than it does to destroy some cavity nesting habitat. (Alternatives for managing aspen forests are discussed in PART IV. MANAGEMENT.)

Birds of Prey

Three species of accipiters, three of buteos, four falcons, the golden eagle, and the turkey vulture are found in aspen forests in the West. Also, there are six species of owls, varying in size from the northern pygmy to the great horned (see the chapter appendix). This variety illustrates the biological richness of this forest type. Prey, in the form of small mammals and other birds, is abundant in the aspen forest. This abundant food source attracts these species at the top of the food pyramid.

Perhaps the greatest variety of predaceous birds inhabit the mixed aspen-conifer forest. Many hawks nest in this habitat. Also, unless they can hide in burrows, owls are more likely to be encountered in the mixed forest, roosting in dense conifers in the daytime. In contrast, feeding areas for many predaceous birds are predominately in the pure aspen forest or in nearby open brush, meadows, and grasslands.

Most raptors and owls will nest in the aspen type. The golden eagle, and the peregrine and prairie falcons are least likely to be found nesting in the forest, but are most apt to be nesting on some open, precipitous rocky area in the vicinity (Harrison 1979). Others, such as the cavity nesting species, seem to prefer aspen for nest sites, although the merlin, listed as a cavity nester, probably will nest in the rocky bluffs with the other large falcons. The buteos will nest in the aspen or mixed forest, but will do much of their hunting in more open terrain. The accipiters will nest and hunt in the forest. The largest of these, the goshawk (fig. 3), and the largest owl, the great horned, are very effective predators of small game (grouse and hares) in the aspen forest.

Figure 3.—An active northern goshawk nest in a mixed aspen-conifer stand in western Wyoming.

Game Birds

Mourning Dove

Most mourning doves nest at lower elevations, beneath the zone of montane aspen. Where doves are found with aspen, however, they nest in tall shrubs and aspen trees. Because doves are ground-feeding granivores that prefer open areas for feeding, they commonly are encountered along the forest edge and in small groves of trees bordering agricultural lands and rangelands. This species is an early migrant, departing from most aspen habitats in late August or early September. Aspen appears to be incidental to habitat requirements of mourning doves throughout most of their range.

Band-tailed Pigeon

Band-tailed pigeons nest in the mountains within the southern range of montane aspen, from central Utah and Colorado southward. According to Harrison (1979), they prefer to nest in broadleafed trees; therefore, aspen may be chosen for nesting. However, they feed on acorns and berries, and are generally found in the Gambel oak and ponderosa pine zone, at an elevation below that where aspen commonly grows (Jeffrey 1977).

Wild Turkey

The range of the wild turkey and that of aspen overlap in the southern Rocky Mountains, especially in Arizona and New Mexico. This ground-nesting bird prefers the coniferous and pine-oak forests of the mountains (Harrison 1979).

Turkeys will use the mixed aspen-conifer type;[3] but, they basically inhabit the ponderosa pine and bordering types (Hoffman 1968). The turkey is a seed-eater that does well where a reliable supply of mast and grass seeds are available. They also forage on insects, which are abundant in the aspen type (Winternitz 1980), and on many of the forbs and grasses available in the typical aspen understory (Korschgen 1967).

Sharp-tailed Grouse

The sharp-tailed grouse in the parklands aspen habitat will use aspen trees in the winter and spring; but they prefer and select grassland and grassland-low shrub cover throughout most of the year. During the winter, small aspen and shrubs offer this grouse protective cover and food. They feed on aspen buds in winter and spring (Hamerstrom 1963, Moyles 1981). Aspen is useful as small thickets of young growth (3–6 feet (1–2 m) tall) and as larger patches of taller trees for winter use (Evans 1968, Hamerstrom 1963). During much of the year, aspen, except as a shrub, seems to be of little or no importance, perhaps even a detriment, to the sharp-tailed grouse. The presence of aspen near breeding arenas discourages their use (Moyles 1981). Moyles (1981) cited evidence that invasion of grassland by aspen reduced sharp-tailed grouse habitat.

The sharp-tailed grouse is characteristic of early successional stages in the aspen ecosystem. They frequently utilize burned areas in which aspen regeneration is mostly shrub-sized, with some very scattered stands of mature trees that have escaped the fires. As extensive stands of trees return, the sharp-tailed grouse gives way to the ruffed grouse.

Blue Grouse

In contrast to the sharp-tailed grouse, the blue grouse is prevalent in areas that are successionally beyond the aspen stage, where much of the landscape is occupied with conifers. However, the conifer forest is particularly important only in winter, when blue grouse roost in the dense conifers and feed primarily upon conifer needles (Beer 1943, Hoffman 1961, Stewart 1944). During summer, blue grouse prefer openings, usually at lower elevations, that are vegetated with grasses, forbs, shrubs, and aspen patches. Relatively dense grass-forb mixes are chosen first, and shrubs second (Mussehl 1960, 1963). There they nest, raise their broods, and feed upon insects, fruits, and leaves.

[3]*Personal communication with David R. Patton, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station's Forestry Sciences Laboratory in Tempe, Ariz.*

Aspen is not an essential part of blue grouse habitat; healthy populations are found where no aspen exists. However, wherever aspen is an extensive component of the summer and early fall home range of blue grouse, it provides significant food and cover for developing grouse broods, if it is not too heavily grazed.

Ruffed Grouse

The ruffed grouse has a wide range across North America (Aldrich 1963), is associated with hardwood and hardwood-conifer mixed forests, and is primarily a bird of the aspen and associated forest types (fig. 4).

Gullion (1977a) suggested an obligatory relationship between ruffed grouse and the aspen type wherever snow covers the ground between November and April. Aspen is heavily utilized as food and as cover throughout most of the year (Doerr et al. 1974, Phillips 1965, Schladweiler 1968) (fig. 5), providing a highly nutritious food source (Gullion and Svoboda 1972), protection from the weather (Bump et al. 1947), and escape from predators (Gullion et al. 1962). About 75% of the annual grouse harvest is taken in the six states and provinces where aspen is most abundant (Gullion 1977a). Ruffed grouse, however, are found in huntable populations in hardwood forest habitats south and west of the range of aspen (fig. 4).

Wherever aspen and grouse ranges overlap in the West, this grouse selects aspen habitat during part or all of the year[4] (Doerr et al. 1974; Landry 1982; Phillips 1965, 1967; Rusch and Keith 1971). However, this aspen community must possess suitable density and structure to make it good grouse habitat.

Aspen and associated hardwoods are important components of the habitat during the breeding and nesting season. Males select drumming logs that are under a dense overstory and are surrounded by a relatively dense shrub understory but with good horizontal visibility (Berner and Gysel 1969, Gullion et al. 1962, Landry 1982, Robertson 1976), giving them maximum protection from predators as well as visibility to receptive females. The hens choose similar cover for nesting; but, after hatching, they move their broods to areas with relatively open canopies and well-developed and dense herbaceous understories[4] (Landry 1982). In the mountain West, the broods move downslope as the season progresses, and are often found during late summer in the relatively moist and dense cover along stream bottoms (Hungerford 1951, Marshall 1946, Robertson 1976).

The foods used by ruffed grouse vary with season, age of bird, and availability of plant species; but usually include aspen, if it is a component of the habitat. The chicks feed exclusively upon insects for their first 5 weeks, which partially explains why broods select the insect-rich, dense, herbaceous understory. About 7 weeks after hatching, they assume an adult diet and

[4]*Stauffer, Dean F. and Steven R. Peterson. 1982. Seasonal habitat relationships of ruffed and blue grouse in southeastern Idaho. 138 p. Final report (unpublished). Forest, Wildlife, and Range Experiment Station, University of Idaho, Moscow.*

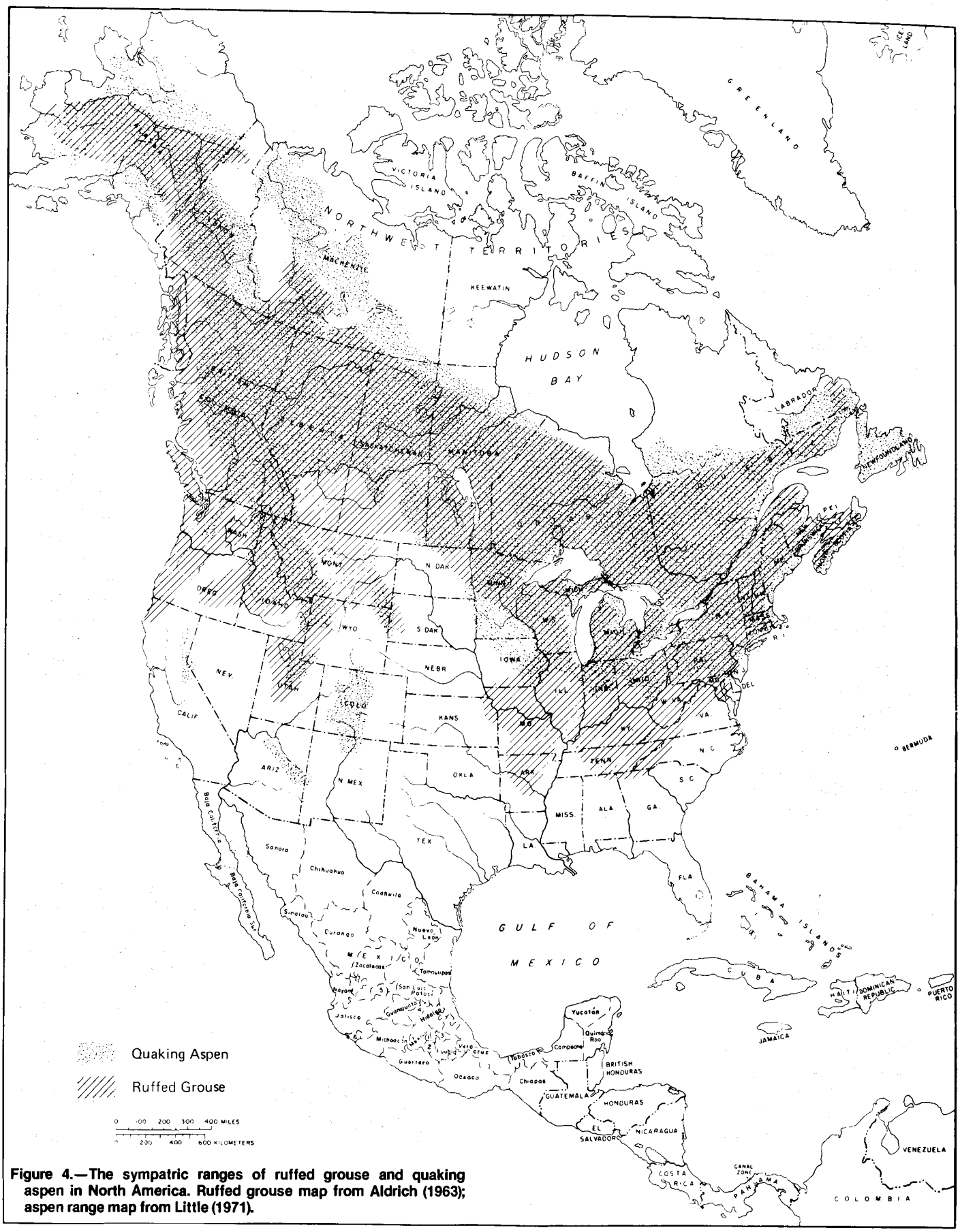

Figure 4.—The sympatric ranges of ruffed grouse and quaking aspen in North America. Ruffed grouse map from Aldrich (1963); aspen range map from Little (1971).

feed primarily on plant parts. Incubating hens eat aspen leaves and catkins (Maxson 1978, Schladweiler 1968). Gullion and Svoboda (1972) found that drumming males chose logs within sight of male aspen, which probably were used as a food source. Svoboda and Gullion (1972) stated that, in Minnesota, spring foods consisted mainly of staminate aspen buds and catkins. Adult grouse in summer feed on a variety of abundant plant materials—seeds, fruits, and leaves. In northern Utah, Phillips (1967) found that rose hips and aspen leaves made up 50% of the autumn diet. After leaf fall, and certainly after snow covers the understory, aspen twigs and buds, especially the male floral buds (Svoboda and Gullion 1972), become a dominant part of the grouse diet (Doerr et al. 1974, Phillips 1967). Willow buds, chokecherry buds, rose hips, and other available foods also are used in varying amounts (Doerr et al. 1974, Marshall 1946, McGowan 1973, Phillips 1967).

Aspen buds alone are nutritious enough to support grouse during the winter (Svoboda and Gullion 1972), especially the staminate floral buds in the upper part of the canopy (Gullion and Svoboda 1972). However, willow buds contain a greater concentration of protein and carbohydrates but less fats than aspen in winter (Doerr et al. 1974), and rose hips are especially high in protein (Welch and Andrus 1977), making them good supplements to a steady diet of aspen buds in winter and spring.

Figure 5.—Aspen floral buds are an important food for ruffed grouse. (Photo by Tom Martinson)

Breeding and nesting habitat of ruffed grouse is generally dense, pole-sized stands of aspen or mixed hardwood cover of similar structure. The dense herbaceous understory chosen by broods in summer perhaps develops best under open canopies. Solitary grouse use thickets of shrubs in spring and summer, which provide protection from precipitation, extreme temperatures, and predators (Landry 1982, Robertson 1976). In autumn, birds use diverse cover, but still prefer aspen.[4] Mixed hardwoods with brushy overgrown edges often are chosen (Berner and Gysel 1969, Robertson 1976). In winter, when there are deep snowpacks throughout most of the mountain West, ruffed grouse are found in the aspen and aspen-conifer types. During this season, the grouse use stands of trees larger than those used in spring and summer, perhaps to feed upon the abundant floral buds on mature aspen. At times, grouse are found in dense stands of conifers, where they sometimes roost.[4]

MAMMALS

The aspen ecosystem in western North America provides habitat for at least 55 species of wild mammals (see this chapter's appendix). In size, these range from the dwarf shrew to the bison. Some species occur in the aspen type as well as in many other vegetation types; others prefer the aspen forest. Those species that appear to select the aspen type, and those that are currently important as game, or for esthetics, or that have obvious or economic impact on the plant community are discussed in this chapter. These include moose, elk, deer, snowshoe hare, cottontail rabbit, beaver, porcupine, and pocket gophers.

Moose

The largest member of the deer family, the moose, makes extensive use of the aspen ecosystem (fig. 6). The range of moose and the more northerly range of aspen in North America coincide. The use of aspen and associated vegetation by moose is much more than random. Usually, moose first select willow and then aspen as browse.

Moose are primarily browsers, especially in winter. On most western ranges, they seem to concentrate on willows; in the East they often select aspen, birch, and balsam fir for browse (Peek 1974b). Forbs may be heavily used during summer and fall; but grasses seldom are a primary food source. Peek (1974b) cited studies that listed aspen among the most important species of browse in southcentral Alaska, Alberta, British Columbia, Manitoba, Minnesota, Montana, and on Isle Royale National Park in Lake Superior.

The Shiras moose, the subspecies which occupies the montane woodland of the western U.S. and adjacent Canada, has a variety of winter ranges: (1) floodplain willow bottoms, (2) willows and conifers along mountain streams, (3) aspen and conifer stands in the absence of willows, (4) pure conifer stands, especially with subalpine fir, and (5) sometimes the northern desert scrub (Peek 1974a). Where willows are its primary source of food, as on floodplains, there may be little need to consider the aspen type as essential moose habitat. But where moose use the upland types, the aspen ecosystem becomes important habitat.

Many of the understory shrubs in the aspen type are palatable and sometimes important moose browse (Peek 1974b). Browsing varies widely among the conifers associated with the aspen ecosystem. Spruces are virtually untouched by moose, lodgepole pine sometimes is used, Douglas-fir often is consumed, and subalpine fir is a preferred browse (Gruell 1980, Gruell et al. 1982, Stevens 1970).

Because the niches for moose and other cervids (elk and deer) differ, they compete very little in forested habitats of the West. Moose winter in bottoms and upland forested areas, and they eat mostly browse; elk winter in open areas with less snow and eat herbaceous material, if available (Stevens 1974). Both will use aspen browse; but elk seldom use much willow—the moose's favorite. Although both moose and deer are browsers, in typical mountainous habitats, any competition would occur mostly on the summer range. Usually food is abundant then, and both animals may browse on the same upland plant species without much interspecific competition. In winter, when snow crowds deer onto low-elevation ranges, moose often remain in willow bottoms, aspen patches, and conifer stands at higher elevations where snowpacks may be as much as 30–40 inches (75–100 cm) deep (Kelsall and Telfer 1974).

Probably because of their tolerance for cold, moose will occupy willow bottoms without much thermal cover early in winter. But, as winter progresses and snowpacks deepen, they move into densely forested uplands with less snow (Rolley and Keith 1980). Moose in Alberta selected upland aspen less than 33 feet (10 m) tall as preferred habitat, but used tall aspen and aspen-conifer mixes at about their level of availability (Rolley and Keith 1980).

Gordon (1976), in Montana, described ideal upland moose habitat as having a good distribution of aspen and associated trees and shrubs in a mosaic of age classes. Conifer patches for hiding cover also are desirable.

Regeneration of young vigorous stands of aspen, willow, and associated shrubs, usually after fires, improves moose habitat and results in a moose population increase (Gruell 1980, Gullion 1977b, Irwin 1975, LeResche et al. 1974). After this browse grows out of reach, the moose population decreases. LeResche et al. (1974) noted that fire-induced seral communities in Alaska had the greatest moose population densities, but that these were unstable and ephemeral.

Moose are well adapted to the aspen ecosystem. Where moose and aspen coexist in the West, it appears that young stands of aspen suckers provide the most browse, pure aspen stands of large trees provide some understory forage, and older seral stands with conifers offer cover and some browse, sometimes of choice subalpine fir. Community types with an abundance of shrubs and forbs in the understory perhaps are most valuable as moose habitat. Because conifers also provide some browse as well as escape or hiding cover, perhaps seral aspen stands are best. However, where willows are abundant in areas that can be used by moose throughout the year, the aspen is supplemental, not an essential part of moose habitat on this western range.

Figure 6.—The Shiras moose uses aspen and aspen-conifer forest cover extensively during all seasons of the year, in several western states. (Photo by Clay Perschon)

Elk

Elk is the second largest herbivore found in the aspen type. Thomas and Toweill (1982) provided a comprehensive review of the ecology and management of this animal in North America. Where concentrated, elk have considerable impact on the aspen ecosystem (see the ANIMAL IMPACTS chapter). The range of the Rocky Mountain subspecies of elk and the range of aspen in the West are similar. Rocky Mountain elk, however, do not depend on aspen as critical habitat throughout their range. Large and healthy herds of elk exist where aspen is only a minor component in the vegetation complex, such as in northern Idaho. Nevertheless, where aspen and elk occur together, the elk appear to select the aspen type over several other available habitats (fig. 7). At least in southern Idaho, elk were found in the aspen in much greater frequency than would be expected from random use.[5]

In the central Rocky Mountains, where aspen is most extensive, most of the aspen zone is at an intermediate elevation between elk winter and summer ranges.

[5]*Personal communication with Lonn Kuck, and data on file at Idaho Game and Fish Department, Soda Springs, Idaho.*

Where aspen occurs on elk winter range, it is very heavily utilized by concentrations of these large cervids. Excellent examples of this can be seen in Rocky Mountain National Park in Colorado and at the National Elk Refuge near Jackson, Wyo. Aspen stands that exist on spring migration routes also are heavily browsed. Autumn migration has a lesser impact on the trees, because palatable herbaceous vegetation is more abundant. Consumption of aspen and associated understory species by elk on summer range is usually well distributed and quite light. Often, elk spend their summers at higher elevations, above the aspen zone, where they graze in meadows and use coniferous forest stands for cover.

Elk, particularly the Rocky Mountain subspecies, primarily graze. They consume essentially the same grass and forb species as do cattle. Where production of palatable herbaceous species is low, or when snowpack depths exceed 20 inches (50 cm), the elk will feed extensively on browse. According to Nelson and Leege (1982), elk prefer grasses, then forbs; and, as curing or loss of herbaceous material occurs, they will use deciduous browse species first and coniferous browse last.

Aspen is avidly sought from among the browse species. It is consumed in excess of its proportion in the vegetation and is often a major part of the elk diet. It is considered a highly valuable browse species in winter, spring, and autumn; and, if browse is used much, it is a valuable species in summer as well (Kufeld 1973, Nelson and Leege 1982). The qualitative value of aspen and associated plants as ungulate food is discussed in the section on deer. However, among the browse species selected by elk in winter, aspen had the highest percentage (39–47%) of digestible dry matter (Hobbs et al. 1981).

An aspen understory rich in forbs and grasses provides excellent quality elk feed in large quantities during the summer and early fall seasons (see the FORAGE chapter). During those seasons the aspen provides cover as well. In fall and winter, if the elk remain in the aspen zone, they will browse aspen to a height of approximately 6 feet (2 m) and will chew the bark from mature aspen trees (see the ANIMAL IMPACTS chapter). Dense stands of young aspen are valuable browse; but, this resource is ephemeral. Aspen suckers, if growing in the open and not browsed, will extend their crowns above the reach of elk in 6 to 8 years (Patton and Jones 1977).

Figure 7.—Elk are an important resource in the aspen forest type in the Rocky Mountain West. (Photo by Kem Canon)

Elk often need hiding or security cover (Thomas 1979). Although their need for thermal cover is not clear (Peek et al. 1982), they utilize it where available. Aspen-conifer mixed stands provide both cover and forage all year. Aspen stands with a dense shrub understory provide hiding cover, whereas pole-sized or larger dense conifer stands provide the best thermal cover (Thomas 1979). In contrast, pure aspen forests provide substantial cover only during summer. When dormant, mature aspen provides poor hiding cover and almost no thermal cover. In summer, the combined values of good forage and cover in the aspen forest make it especially valuable to elk. Elk then prefer the aspen stands to adjacent clearcuts that have even more palatable forage (Collins and Urness 1983).

Aspen habitat can be important during the calving season. In the spring, during the up-slope migration of elk, the pregnant cows break off from the herd several days before parturition. They usually calve and then remain in the mid-elevation forest zone for several weeks before rejoining the herd. Aspen often is a predominant forest type in this mid-elevation zone. Thus, aspen and associated vegetation provides critical cover and forage for these cow elk and young calves.

Deer

Either mule deer (Wallmo 1981) or white-tailed deer are common throughout the range of aspen in the western United States. They are less common farther north, but still prevalent in many aspen areas. The mule deer predominates in the states with the most aspen (table 1). Mule deer herds in these states are migratory—they spend summers at high elevations within the aspen zone and winters on steppe and brushlands at lower elevations, usually below the aspen zone. For the most part, aspen is summer and fall range for deer in the mountainous, semiarid West. Exceptions are where aspen grows on lands without deep winter snowpacks.

Deer utilize aspen both as cover and as browse. Many herds, especially in Colorado and Utah, are found in the aspen forest type throughout much of the summer (fig. 8). Whether or not aspen is a critical habitat component depends upon the other facets of their habitat. If adequate forage and cover exist in tall shrub types, or in a mosaic of conifer patches and openings, then the aspen type may not be critical to their welfare. Pure conifers provide cover, but little forage; openings provide forage but no cover. Aspen, in summer, provides both.

Much emphasis in both research and management has been placed upon the availability of quality forage on the winter ranges of wild ungulates. The well-being of these animals often is at least equally dependent upon their summer and fall ranges. Deer herds on good sum-

mer range, in the aspen and associated vegetation types, are more productive and healthier than those herds forced to use overgrazed and deficient summer ranges (Hungerford 1970, Julander 1962, Julander et al. 1961). Their survival through winter, when their metabolism and level of activity is lowest (Moen 1978), depends largely upon fat stores built up in late summer and autumn.

In contrast to elk, deer primarily browse throughout much of the year. Only in spring and summer, when succulent herbaceous forage is abundant, do deer consume more herbaceous plants than they browse. Like the elk, they migrate up the mountains while following the wave of new spring and summer herbaceous growth. Forbs are very much preferred. As summer progresses and the herbaceous material cures, the deer shift progressively to browse.

Aspen was among the top eight species of preferred browse for Rocky Mountain mule deer and, if available, was moderately used in winter, spring, and summer, and heavily used in autumn (Kufeld et al. 1973). Hungerford (1970) noted that aspen sprouts became a key food only after new growth matured, usually in July. Whenever available, leaves were selected from mature aspen trees. Upon leaf fall in autumn, deer consumed large quantities of aspen leaves (Julander 1952). In addition to the aspen itself, deer commonly ate several associated understory shrubs: serviceberry, barberry, pachistima, common chokecherry, rose, willow, and especially snowberry. The most used forbs in the aspen forest understory were western yarrow, aster, milkvetch, fleabane or daisy, geranium, peavine, lupine, knotweed, cinquefoil, common dandelion, valerian, and American vetch (Collins 1979, Kufeld et al. 1973).

The quality of forage taken from the aspen type by deer and elk is quite high, especially in summer. The mix taken by deer and elk in Utah during the growing season was about 65% digestible and contained 13% protein (Pallesen 1979). Protein contents of 21% for deer diets and 18% for elk diets on an aspen dominated site were measured in a later study (Collins and Urness 1983). Some shrubs in the aspen type are very nutritious. For example, rosehips have a high nitrogen free extract (60%) and are readily browsed by mule deer (Welch and Andrus 1977).

Figure 8.—In the West, mule deer are the most common big game inhabiting the aspen forest type.

The nutritive value of aspen alone compares very favorably with several other plant species important to mule deer (Short et al. 1966). They found the protein contents of aspen varied from a high of 17% in spring to 6–10% by leaf-fall in autumn; in winter, crude fat was 15–19%, caloric values were 5 calories per gram, and carotene contents were 14–18 μg per gram.

Aspen leaves are used by browsing animals during summer. Their nutrient content is high, changes during the growing season, and varies from clone to clone (Tew 1970b). Tew (1970b) found green aspen leaves to contain 12% protein, 10% fat, 2.3% Ca, 1% K, and 7.5% ash in late summer, during what is usually the peak of the summer browsing-grazing season. Upon leaf drop in the autumn, they have approximately the following nutrient contents; 1.9% Ca, 0.4% N (only 3% protein), 0.4% K, 0.1% Mg, 0.05% P, and 5.3% ash (Bartos and DeByle 1981).

Aspen bark is 50% digestible by ruminants (Baker et al. 1975), apparently palatable, somewhat nutritious, comparatively soft, and readily chewed from the tree. The nutrient content of aspen bark is: 0.5% N, 0.06% P, 0.3% K, 1.6% Ca, 0.1% Mg, and 5.0% ash (Bartos and Johnston 1978).

The production of forage in large quantities in the aspen understory usually is more important to deer on their summer range than is the production of aspen browse itself. The quantity and quality of this food production is examined in the FORAGE chapter, and can be inferred from the cited digestibility and protein values (Collins and Urness 1983, Pallesen 1979).

In comparison to larger ungulates, deer carefully select leaves and succulent portions of forbs, browse, and some grasses. Coarse material is left. The aspen understory commonly has a broad selection of palatable deer forage. Deer gravitate to it and to the cover provided by the aspen overstory (Collins and Urness 1983).

Deer make greatest use of the aspen type during summer and autumn, when aspen and associated deciduous shrubs are in full leaf, and both thermal and hiding cover are abundant. Aspen communities on the shrub-steppe western range are second only to the riparian zones in value to mule deer (Leckenby et al. 1982). Forage provided by the understory plus thermal cover provided by the overstory make this type especially attractive to deer in summer. They prefer to feed in the aspen forest rather than in clearcut openings that have twice as much forage. They commonly bed down in the aspen forest also (Collins and Urness 1983).

In terrain typical of the mountain West, deer appear to prefer habitats that are close to a water supply, especially in late summer, when forage elsewhere is cured. The aspen forest with a good understory of palatable shrubs and forbs, if near a stream or spring, is ideal summer deer habitat. McCulloch compared deer population densities in aspen, ponderosa pine, mixed

conifer, spruce-fir, and meadow habitats in Arizona.[6] Greatest densities were found in aspen, especially where there was abundant forage.

The cover value of aspen and other deciduous species decreases markedly as they lose their leaves in autumn. Thermal cover probably is not needed then because of moderate temperatures; but hiding cover may be essential, especially during the hunting season. Mixed aspen-conifer stands, aspen with a dense understory of tall shrubs, and pure conifer patches then become important deer cover. Dense stands of aspen regeneration also provide good escape cover as well as forage in this season.

With the onset of winter and the accumulation of a snowpack in the mountain West, the cover value of aspen for large ungulates becomes negligible. Dense stands of small trees offer cover and browse; but only conifers provide good thermal cover in winter. Snowpacks deeper than 12–16 inches (30–40 cm) force deer to migrate to lower elevations and generally out of the aspen forest zone. Therefore, except for a brief period in late autumn, dormant aspen stands provide little cover where deep snowpacks accumulate.

Snowshoe Hares

Snowshoe hares may be present throughout most of the aspen range in the West (fig. 9). This animal, however, is more common in the associated coniferous forests. In the Rocky Mountains, winter hare habitat is lacking in most pure aspen stands because of deep snowpacks. In northern Utah, Wolfe et al. (1982) found 85% of winter use by hares was in vegetation types that had cover densities immediately above the snowpack of at least 40%. Sometimes aspen with a very dense understory of tall shrubs fits this criterion; but usually only conifers have this much cover in winter.

During summer, snowshoe hares disperse somewhat from coniferous winter cover (Wolff 1980). During the growing season, the aspen type provides adequate cover and excellent forage. Aspen is nutritious and choice food for hares (Walski and Mautz 1977), although new suckers, with high terpene and resin contents, may not be as palatable as twigs on the mature growth (Bryant 1981). During summer, snowshoe hares shift largely to a diet of succulent plant material (Wolff 1980). Because the aspen type has much more herbaceous and shrub cover than most coniferous types, in summer it probably is a more desirable habitat.

Snowshoe hare populations are cyclic in the northern part of their range. During population peaks in Alberta, Pease et al. (1979) found that browsing by hares was so great that food supplies became limiting. About 50% of the woody stems were severely browsed during the peak; but only 2% were being browsed 2 years later, after the population declined drastically. Aspen was among the six most common browse species.

Figure 9.—Aspen stands with an appreciable conifer component provide snowshoe hares with satisfactory habitat, even in winter, when deep snow buries much of the understory cover and food.

The aspen type, if well interspersed with dense conifer patches, provides adequate snowshoe hare habitat in the West. Marginal habitat is provided with aspen and a dense understory of tall shrubs, if this understory is not covered with deep winter snowpacks. It is doubtful if even the peak density of aspen suckers and shrubs on most aspen clearcuts in the West provide adequate snowshoe hare habitat in winter (Wolfe et al. 1982).

Cottontail Rabbits

Most aspen in the western United States is at elevations above the zone where cottontail rabbits are commonly found. Snowpacks may be too deep and the winters too severe for cottontails in these environments. Cottontails are found in aspen groves at lower elevations and where aspen is associated with sagebrush and similar shrublands. On these sites, dense aspen patches in mesic pockets or seepage areas within an otherwise rather exposed environment provide thermal and hiding cover for cottontails and other wildlife, especially in winter. In contrast, the cottontail in the East and Midwest finds the aspen habitat quite suitable, and is often abundantly found in recent cutovers that are well-stocked with aspen suckers (a good food source in winter) and logging slash used for hiding cover.

[6] *McCulloch, Clay Y. 1982. Evaluation of summer deer habitat on the Kaibab Plateau. Final Report, Arizona Game and Fish Department, Project W-78-R, 20 p. [Typescript]*

Beavers

Of the larger mammals considered here, beavers are the only ones restricted for almost their entire winter food supply to aspen and to other species in the family Salicaceae. Although beavers use other hardwoods, such as alders and maples, most beaver colonies in the mountainous West are found on streams that flow through or adjacent to aspen or willow (fig. 10). Both species are commonly used (although aspen is preferred) for food and for dam construction (Hall 1960). (See the ANIMAL IMPACTS chapter for a more complete discussion of the aspen-beaver relationship.)

Aspen, because it is an upland hardwood type, provides essential habitat for beavers along streams that do not have sufficiently wide riparian zones to support an adequate supply of willow or cottonwood. Many of the streams in the West, especially in their upper reaches, fit this description. There, beaver are found only where there is aspen.

Beaver populations along any given reach of stream are not stable. They move in, establish a series of dams and lodges, harvest the aspen and willow within reach of these inundated areas, and then depart after the supply is exhausted. This is especially true in the aspen habitat, where sucker regrowth is not fast enough to sustain the beaver population (Hall 1960). Willow is better for sustaining relatively stable beaver populations along low-gradient streams, because it sprouts prolifically after cutting and grows rapidly in the sometimes inundated riparian zone. However, on high-gradient streams, aspen may be superior to willow for dam construction (Gruell 1980).

Beaver will cut any diameter aspen available (fig. 11), although they seem to have a slight preference for the 2-inch (5-cm) size class (Hall 1960). About 2–4 pounds (1-2 kg) of bark is eaten each day by a mature beaver, most of which comes from branches and boles less than 3-4 inches (8-10 cm) diameter (Hall 1960, Stegeman 1954). Stegeman (1954) found that the degree of utilization varied from 98% on 3/4- to 1-inch (2- to 3-cm) trees to 64% on trees larger than 8 inches (20 cm) diameter. The small trees produced only about 2 pounds (1 kg) of food, whereas 10-inch (25-cm) diameter trees produced 220 pounds (100 kg) of beaver food. He estimated that 1,500 pounds (700 kg) of aspen food is required per beaver per year. In summer beavers feed on succulents, too. Tree cutting and food cache construction by beaver reaches a peak in autumn (Hall 1960). Banfield (1977) estimated that about 200 aspen trees would support one beaver for 1 year.

Figure 10.—A beaver dam and lodge in the pure aspen forest type, along a stream in Utah's mountains.

Figure 11.—An 8-inch diameter aspen felled by beavers during the previous week. The bark and twigs were eaten, and some branches were removed and used in the nearby lodge and dam.

Beaver cutting may extend a considerable distance from water, 100–650 feet (30 to 200 m), depending upon topography, food availability, and the behavioral characteristics of the colony. Therefore, potential beaver habitat in the aspen type would be a strip perhaps 650–1,000 feet (200–300 m) wide along each relatively placid perennial stream, with greater distances in bottomlands with a potential for extensive flooding by beaver dam construction. Greatest utilization of the aspen in this zone would be in dense stands of trees from 2 to 6 inches (5 to 15 cm) in diameter.

Porcupines

Porcupines are associated with a variety of woody vegetation types in the West, from conifers to sagebrush. Although this large rodent appears to have preference for some tree species, such as hemlock or basswood (Curtis 1941, Krefting et al. 1962), many species, including aspen (Lynch 1955), are commonly barked and appear to suffice as a winter food source (see the ANIMAL IMPACTS chapter) (fig. 12). During summer the porcupine also feeds on succulents, and then will readily eat aspen leaves if available (Banfield 1977). Because predation is not a serious consideration for this quill-covered animal, its use of cover probably is largely for physical comfort. It uses ground shelters (rocks, hollow logs, caves, etc.), especially in winter and for reproduction (Banfield 1977, Thomas 1979).

Pocket Gophers

Although the pocket gopher is seldom seen, evidence of this fossorial rodent is present in most aspen stands. This evidence consists of small soil mounds that are pushed to the surface during summer feeding and burrow building. In winter, mineral soil is deposited in elongated castings at the base of the snowpack. (See the ANIMAL IMPACTS chapter for more detail.)

Figure 12.—Porcupines feed on aspen and associated vegetation.

Pocket gophers perhaps are the most important member of the small mammal community in aspen forests in the West. Among the small mammals, they are comparatively large, 1/4 to 1 pound (100–500 gm), and often dominate the small mammal biomass (Andersen et al. 1980). Population densities of 36 or more individuals per acre (90 per ha) can be reached in very favorable habitats, such as meadows (Andersen and MacMahon 1981), beyond which intraspecific competition for territory may limit densities (Miller 1964). In the aspen type of northern Utah, Andersen and MacMahon (1981) found population densities varied from 1 to 13 gophers per acre (2 to 33 per ha) over a 4-year period. This was less than found in nearby meadows but markedly more than found in coniferous forest.

Forbs are the primary food of pocket gophers; indeed, forbs may be an essential food for the northern pocket gopher (Miller 1964). This may explain the abundance of gophers in the forb-rich aspen forest type. Gopher diets in summer consist of more than 75% aboveground plant parts; but their winter feeding activity is almost entirely restricted to roots and rhizomes (Ward and Keith 1962).

Population densities of gophers apparently are controlled by winter food supply and by soil conditions. When soils are not frozen solid nor saturated, gophers will burrow in the surface 6 inches (15 cm) of soil at a rate of 3/4 inch (2 cm) per minute and feed on whatever roots, especially forbs, are encountered (Andersen and MacMahon 1981). Andersen and MacMahon (1981) calculated that enough food material was present in the aspen forest to sustain pocket gophers with only 4 hours of feeding-burrowing per day. Hard frozen soil will stop all burrowing activity; but, aspen soils seldom freeze under the deep snowpacks typical in the mountainous West. However, when they do freeze, food caches may become critically important. Aspen soils seldom are too wet for burrowing, except during spring snowmelt, when portions of abandoned gopher burrows have been observed to carry runoff water (Andersen and MacMahon 1981).

Sites with well-drained and friable soils that are protected from freezing solid by topographic position or by deep snowpacks, and with abundant vegetation containing a large component of forbs, appear to be the best pocket gopher habitat (Andersen and MacMahon 1981, Miller 1964). Many aspen stands in the West fit this description perfectly. Only mountain meadows that are well drained and rich in forbs are better habitat.

Other Small Mammals

This composite category includes shrews, mice, voles, ground squirrels, tree squirrels, and chipmunks. There are five species of shrews, three of mice, five of voles, four of ground squirrels, two of tree squirrels, and four species of chipmunks in the aspen forests of the West

(appendix). Some of these species are restricted to aspen stands that contain a substantial conifer component; others occur in pure aspen.

Rodents are the most numerous, large, primary consumers of plant energy. In the coniferous forest, deer mice, chipmunks, and red-backed voles are notable consumers of conifer seed (Radvanyi 1973). This probably is true in mixed aspen-conifer forests, too. Small mammals often have two or more litters per year, young mature in a couple months, and populations turn over rapidly. Population densities respond quickly to food availability, habitat changes, and weather. Small mammals are the most important food source for terrestrial carnivores (Halvorson 1981).

The deer mouse usually is the most abundant of all small mammals caught during trapping studies in aspen forests (Andersen et al. 1980, Hanley and Page 1982, Thammaruxs 1975). It is a generalist; 65-75% of its diet consists of seeds (Williams 1959); and it does well in the relatively open aspen forests. Another species, the least chipmunk, has similar habitat requirements, and often is found in near-equal abundance (Andersen et al. 1980, Hayward 1945, Thammaruxs 1975). The red-backed vole is restricted to forested habitats. It is quite abundant in dense aspen (Thammaruxs 1975), but probably most numerous in conifer forests (Halvorson 1982). Populations of this vole decline markedly if the forest is clearcut or burned[7] (Halvorson 1982). These declines often coincide with increases in deer mouse populations after forest removal.

On some aspen forest sites, the western jumping mouse is a common member of the small mammal population (Stinson 1977, Thammaruxs 1975). It, like the deer mouse and chipmunk, is a seed-eater. Voles, however, consume both seeds and succulent plant materials.

The flying squirrel, though seldom seen because of its nocturnal habits, also is present in the aspen forest. Andersen et al. (1980) estimated that it made up about 5% of the biomass of the seven most common mammal species found in the aspen type of northern Utah. Perhaps this mammal is even more important in mixed aspen-conifer stands. Flying squirrels are associated with coniferous forests, where they are dependent upon large snags for nesting cavities (Halvorson 1981), and where they may comprise 8–9% of the small mammal biomass (Andersen et al. 1980). At least in the East, both the flying squirrel and the red squirrel use abandoned sapsucker cavities in aspen (Kilham 1971).

The red squirrel is confined to coniferous trees for satisfactory habitat. Conifer cones and buds are its food source. Juvenile squirrels will disperse into the aspen forest; but mortality there is high (Rusch and Reeder 1978). These juveniles apparently either perish or find groves of conifers as habitat. Red squirrels often are found in isolated conifer groves amidst large stands of aspen. Mixed conifer-aspen stands will support good squirrel populations.

[7]*Personal communications from Glenn L. Crouch, USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, Colo., and H. Duane Smith, Brigham Young University, Provo, Utah.*

Predators and Other Mammals

Many different mammalian carnivores inhabit the aspen forest type (see the chapter appendix). The forest provides cover and protection from other predators and humans, but otherwise is not critical. The food base is their critical component. If suitable habitat is present in the aspen type for herbivores, and adequate and relatively stable populations of prey species are encouraged, the predators largely will take care of themselves, assuming that there is no human intervention.

Other animals in this group are omnivores; they may be as dependent upon the vegetation as they are upon a prey base for a food supply. The largest among these are bears. Black bears in Alberta, for example, prefer aspen, aspen-birch, and jack pine forests in summer and fall, presumably because of an abundance of berries in the deciduous forested uplands. Because they den near their fall feeding sites, most of the dens are also in the aspen and aspen-mixed stands (Fuller and Keith 1980, Tietje and Ruff 1980). Gullion (1977b) cited accounts of black bears feeding on aspen buds, leaves, and catkins (fig. 13). In Colorado and in Idaho, DeWeese and

Figure 13.—Black bears eat aspen buds and catkins, as is evident from the repeated climbing of this aspen tree in northern Colorado. (Photo by Gordon Gullion)

Pillmore (1972) reported several instances of black bears climbing aspen trees and robbing bird nests, including those of cavity nesting flickers.

Most predators are wide ranging and show limited affinity for any particular forest type. These species are listed in the appendix as being in the aspen type even though other types may provide equally good or better habitat. For example, the lynx probably prefers coniferous forest in some parts of its range. Other predators, such as the badger and the red fox, find open areas (grass and shrubs) more to their liking. They are found in aspen only incidentally.

Five species of bats are listed as being in the aspen type (see the chapter appendix). Perhaps the large insect populations in this forest type (MacMahon 1980; Winternitz 1980) attract these mammalian insectivores. Although bats may use the forest for feeding, many species use caves for roosting, resting, breeding, and hibernating. Bats, however, will crawl into hollow trees and under exposed flaps of bark for daytime roosting sites (Thomas 1979).

APPENDIX

Wild Mammals and Birds Found in Aspen and Aspen-Conifer Mixed Forests of Western United States and Adjacent Canada.

The mammal list was derived from Andersen et al. 1980; Armstrong 1972, 1977; Durrant 1952; Hanley and Page 1982; Hunt 1979; Jones et al. 1979 (nomenclature); Thammaruxs 1975; Weatherill and Keith 1969; from personal observations by the author; and from personal communications with Curtis Halvorson, U.S. Fish and Wildlife Service, Fort Collins, Colo.; and with H. Duane Smith, Brigham Young University, Provo, Utah. The bird list was derived from Behle and Perry 1975; DeByle 1981; Flack 1976; Smith 1982; Smith and MacMahon 1981; Winternitz 1976; Young 1973; from personal observations by the author; and from personal communications with Virgil E. Scott, U.S. Fish and Wildlife Service, Fort Collins, Colo.; Glenn L. Crouch, USDA Forest Service, Fort Collins, Colo.; Keith Dixon, Utah State University, Logan; and James Brown, USDA Forest Service, Missoula, Mont. Bird nomenclature follows latest AOU Checklist (The Auk 99(3), 1982).

MAMMALS

Scientific Name	Common Name
Sorex cinereus	Masked Shrew
Sorex vagrans	Vagrant Shrew
Sorex nanus	Dwarf Shrew
Sorex palustris	Water Shrew
Blarina brevicauda	Short-tailed Shrew
Myotis lucifugus	Little Brown Myotis
Myotis volans	Long-legged Myotis
Lasionycteris noctivagans	Silver-haired Bat
Eptesicus fuscus	Big Brown Bat
Lasiurus cinereus	Hoary Bat
Sylvilagus nuttallii	Nuttall's Cottontail
Lepus americanus	Snowshoe Hare
Lepus townsendii	White-tailed Jack Rabbit
Eutamias minimus	Least Chipmunk
Eutamias amoenus	Yellow-pine Chipmunk
Eutamias quadrivittatus	Colorado Chipmunk
Eutamias umbrinus	Uinta Chipmunk
Marmota flaviventris	Yellow-bellied Marmot
Spermophilus armatus	Uinta Ground Squirrel
Spermophilus tridecemlineatus	Thirteen-lined Ground Squirrel
Spermophilus variegatus	Rock Squirrel
Spermophilus lateralis	Golden-mantled Ground Squirrel

Scientific Name	Common Name
Tamiasciurus hudsonicus	Red Squirrel
Glaucomys sabrinus	Northern Flying Squirrel
Thomomys talpoides	Northern Pocket Gopher
Perognathus parvus	Great Basin Pocket Mouse
Castor canadensis	Beaver
Peromyscus maniculatus	Deer Mouse
Neotoma cinerea	Bushy-tailed Woodrat
Clethrionomys gapperi	Southern Red-backed Vole
Microtus pennsylvanicus	Meadow Vole
Microtus montanus	Montane Vole
Microtus longicaudus	Long-tailed Vole
Lagurus curtatus	Sagebrush Vole
Phenacomys intermedius	Heather Vole
Zapus princeps	Western Jumping Mouse
Erethizon dorsatum	Porcupine
Canis latrans	Coyote
Canis lupus	Gray Wolf
Vulpes vulpes	Red Fox
Ursus americanus	Black Bear
Ursus arctos	Grizzly Bear
Procyon lotor	Raccoon
Mustela erminea	Ermine
Mustela frenata	Long-tailed Weasel
Taxidea taxus	Badger
Mephitis mephitis	Striped Skunk
Felis concolor	Mountain Lion
Felis lynx	Lynx
Felis rufus	Bobcat
Cervus elaphus	Elk or Wapiti
Odocoileus hemionus	Mule Deer
Odocoileus virginianus	White-tailed Deer
Alces alces	Moose
Bison bison	Bison
Ovis canadensis	Mountain Sheep

BIRDS

Scientific Name	Common Name
Aix sponsa	Wood Duck
Bucephala clangula	Common Goldeneye
Bucephala islandica	Barrow's Goldeneye
Bucephala albeola	Bufflehead
Lophodytes cucullatus	Hooded Merganser
Mergus merganser	Common Merganser
Cathartes aura	Turkey Vulture
Accipiter striatus	Sharp-shinned Hawk
Accipiter cooperi	Cooper's Hawk
Accipiter gentilis	Northern Goshawk
Buteo platypterus	Broad-winged Hawk
Buteo swainsoni	Swainson's Hawk
Buteo jamaicensis	Red-tailed Hawk
Aquila chrysaetos	Golden Eagle
Falco sparverius	American Kestrel
Falco columbarius	Merlin
Falco peregrinus	Peregrine Falcon
Falco mexicanus	Prairie Falcon

Scientific Name	Common Name
Dendragapus obscurus	Blue Grouse
Bonasa umbellus	Ruffed Grouse
Tympanuchus phasianellus	Sharp-tailed Grouse
Meleagris gallopavo	Wild Turkey
Grus canadensis	Sandhill Crane
Columba fasciata	Band-tailed Pigeon
Zenaida macroura	Mourning Dove
Coccyzus erythropthalmus	Black-billed Cuckoo
Otus flammeolus	Flammulated Owl
Otus kennicottii	Western Screech-owl
Bubo virginianus	Great Horned Owl
Glaucidium gnoma	Northern Pygmy-owl
Asio otus	Long-eared Owl
Aegolius acadicus	Northern Saw-whet Owl
Chordeiles minor	Common Nighthawk
Phalaenoptilus nuttallii	Common Poorwill
Aeronautes saxatalis	White-throated Swift
Archilochus colubris	Ruby-throated Hummingbird
Stellula calliope	Calliope Hummingbird
Selasphorus platycercus	Broad-tailed Hummingbird
Selasphorus rufus	Rufous Hummingbird
Sphyrapicus varius	Yellow-bellied Sapsucker
Sphyrapicus ruber	Red-breasted Sapsucker
Sphyrapicus thyroideus	Williamson's Sapsucker
Picoides pubescens	Downy Woodpecker
Picoides villosus	Hairy Woodpecker
Picoides tridactylus	Three-toed Woodpecker
Colaptes auratus	Northern Flicker
Dryocopus pileatus	Pileated Woodpecker
Contopus borealis	Olive-sided Flycatcher
Contopus sordidulus	Western Wood-pewee
Empidonax flaviventris	Yellow-bellied Flycatcher
Empidonax traillii	Willow Flycatcher
Empidonax minimus	Least Flycatcher
Empidonax hammondii	Hammond's Flycatcher
Empidonax oberholseri	Dusky Flycatcher
Empidonax difficilis	Western Flycatcher
Myiarchus crinitus	Great Crested Flycatcher
Tyrannus tyrannus	Eastern Kingbird
Progne subis	Purple Martin
Tachycineta bicolor	Tree Swallow
Tachycineta thalassina	Violet-green Swallow
Stelgidopteryx serripennis	Northern Rough-winged Swallow
Hirundo pyrrhonota	Cliff Swallow
Perisoreus canadensis	Gray Jay
Cyanocitta stelleri	Steller's Jay
Nucifraga columbiana	Clark's Nutcracker
Pica pica	Black-billed Magpie
Corvus brachyrhynchos	American Crow
Corvus corax	Common Raven
Parus atricapillus	Black-capped Chickadee
Parus gambeli	Mountain Chickadee
Sitta canadensis	Red-breasted Nuthatch
Sitta carolinensis	White-breasted Nuthatch
Sitta pygmaea	Pygmy Nuthatch
Certhia americana	Brown Creeper
Troglodytes aedon	House Wren
Regulus satrapa	Golden-crowned Kinglet
Regulus calendula	Ruby-crowned Kinglet

Scientific Name	Common Name
Sialia mexicana	Western Bluebird
Sialia currucoides	Mountain Bluebird
Myadestes townsendi	Townsend's Solitaire
Catharus fuscescens	Veery
Catharus ustulatus	Swainson's Thrush
Catharus guttatus	Hermit Thrush
Turdus migratorius	American Robin
Ixoreus naevius	Varied Thrush
Dummetella carolinensis	Gray Catbird
Toxostoma rufum	Brown Thrasher
Bombycilla garrulus	Bohemian Waxwing
Bombycilla cedrorum	Cedar Waxwing
Sturnus vulgaris	European Starling
Vireo solitarius	Solitary Vireo
Vireo gilvus	Warbling Vireo
Vireo olivaceus	Red-eyed Vireo
Vermivora peregrina	Tennessee Warbler
Vermivora celata	Orange-crowned Warbler
Vermivora virginiae	Virginia's Warbler
Dendroica petechia	Yellow Warbler
Dendroica coronata	Yellow-rumped Warbler
Setophaga ruticilla	American Redstart
Seiurus aurocapillus	Ovenbird
Oporornis agilis	Connecticut Warbler
Oporornis philadelphia	Mourning Warbler
Oporornis tolmiei	MacGillivray's Warbler
Wilsonia pusilla	Wilson's Warbler
Piranga ludoviciana	Western Tanager
Pheucticus ludovicianus	Rose-breasted Grosbeak
Pheucticus melanocephalus	Black-headed Grosbeak
Guiraca caerulea	Blue Grosbeak
Passerina amoena	Lazuli Bunting
Pipilo chlorurus	Green-tailed Towhee
Pipilo erythrophthalmus	Rufous-sided Towhee
Spizella arborea	American Tree Sparrow
Spizella passerina	Chipping Sparrow
Spizella pallida	Clay-colored Sparrow
Spizella breweri	Brewer's Sparrow
Pooecetes gramineus	Vesper Sparrow
Chondestes grammacus	Lark Sparrow
Passerella iliaca	Fox Sparrow
Melospiza melodia	Song Sparrow
Melospiza lincolnii	Lincoln's Sparrow
Zonotrichia albicollis	White-throated Sparrow
Zonotrichia leucophrys	White-crowned Sparrow
Junco hyemalis	Dark-eyed Junco
Euphagus cyanocephalus	Brewer's Blackbird
Quiscalus quiscula	Common Grackle
Molothrus ater	Brown-headed Cowbird
Icterus galbula	Northern Oriole
Pinicola enucleator	Pine Grosbeak
Carpodacus purpureus	Purple Finch
Carpodacus cassinii	Cassin's Finch
Carpodacus mexicanus	House Finch
Loxia curvirostra	Red Crossbill
Carduelis pinus	Pine Siskin
Carduelis tristis	American Goldfinch
Coccothraustes vespertinus	Evening Grosbeak