# 9

# Wildlife in Alpine and Sub-alpine Habitats

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## Introduction

The landscape of western North America is defined by vast areas of striking mountainous terrain. Since settlement, humans have been fascinated and frustrated with these imposing habitats that offer more vertical than horizontal relief. In the old world, humans have used alpine areas for hunting and agriculture since the beginning of recorded history. Europeans and Asians have practiced alpine agriculture for over 10 centuries, cultivating crops and moving livestock up to alpine pastures in summer and down to lower elevations in fall (Bätzing 1991). In North America, our relationship with alpine areas is much more recent. Mountains posed serious barriers to exploration and the development of agriculture in the previous century. Today, however, alpine areas are valued for their intrinsic beauty and wildness, for their recreational potential, and as a refuge from dense urban areas.

The alpine zone consists of rugged, partially vegetated terrain with snowfields and rocky ridges, above the natural treeline. Alpine ecosystems are structurally simple with few plant species compared to most lower elevation habitats. High elevation habitats are characterized by high winds, prolonged snow cover, steep terrain, extremes of heat and cold, and intense ultraviolet radiation. With increasing elevation, time for breeding decreases and environmental stochasticity increases; at the highest elevations, hypoxic conditions add additional energetic living costs. These factors result in short, intense breeding seasons for wildlife, and the need for seasonal movements to and from patchy breeding habitats and wintering areas.

Despite being highly valued for their intrinsic beauty and wildness, alpine vertebrates and their high elevation habitats are a neglected area for research and management. Alpine ecosystems recently have experienced large increases in amount and kinds of human use, and some areas now show significant deterioration. In this chapter, I describe the wildlife communities inhabiting the alpine zone above natural treeline. I describe what is special about high elevation communities, and what is changing. About one third of the vertebrate fauna in the Pacific Northwest is connected to alpine and sub-alpine habitats across one or more seasons. Alpine habitats are essentially vertical islands. Some animals, such as white-tailed ptarmigan, hoary marmots and mountain goats, remain in their high elevation 'islands' year-round, and leave only to travel to other alpine patches. However, the majority of species move to lower elevation habitats at some life history stage. Thus, connectivity is a key ecological process to maintain for alpine wildlife. Anthropogenically-induced changes at both high and low elevations constitute potential threats for alpine animals which are well adapted for extreme conditions, but not so well for increased warming, competition or predation. Alpine sites have the potential to serve as natural experiments that allow 'space for time' perspectives in predicting animal responses to global climate change.

### 1. The Nature, Distribution and Diversity of Alpine Habitats — Global to Local

A mountain is a landmass arising above the general landscape that induces a change in climate that affects vegetation and animal life (Price 1981). The word *alpine* comes from the Alps, and refers to the zone above the natural treeline, with persistent or permanent snowfields, rocky ridges, occasional wind-shaped trees and continuous to scattered tundra vegetation (Love 1970). The treeline, the lower boundary of the alpine life zone, is often fragmented over several hundred meters of altitude (Körner 1999). Several factors define the alpine zone, including elevation, aspect and high relief, but climate is probably the best determinant of where alpine zones begin (Price 1981, Körner 1999). Alpine

*Fig. 1. Sub-alpine flowers in the foreground, open montane forest with hints of tree 'islands', and a spectacular view of snow-capped Mt Rainier in the background. Slide by Steve Ogle (#17), mid to late August 1999.*

climates are characterized by high winds, low temperatures, low effective moisture and short growing seasons (Braun 1980, Billings 1989). Alpine zones increase in elevation from north to south and from coastal areas to interior. Northward across the mid-latitudes of North America, treeline decreases about 152 m (500 ft) in elevation per 160 km (100 mi, Daubenmire 1954). In the Cascades, treeline increases in elevation from about 2000 m (6560 ft) on the west side to 2500 m (8200 ft) on the eastern continental side (Arno 1984). In this chapter, the alpine zone includes two habitat types, alpine treeless and partially vegetated areas at the top, and the sub-alpine, which is the zone between closed upper montane forest and the upper limits of small trees in open parklands.

The global alpine landmass comprises about 4 million km$^2$, about 3% of the global landmass (Körner 1999), an area about half the size of the continental United States (~ 7 million km$^2$, 2.98 million sq. mi.). About 30% of this alpine landmass is vegetated (Körner 1999). In Washington, the total area of alpine and sub-alpine habitat is about 4.4% of the landbase and, in Oregon, about 0.6% (Kiilsgaard 1999). Further north in the Pacific Northwest, 17% of British Columbia is classified as alpine (B.C. Ministry of Forests Database). By global and continental standards, the mountains in Washington and Oregon are modest in elevation. Mt. Everest (8848 m; 29,029 ft) on the Tibet-Nepal border is the highest elevation on earth. Mt. Denali in Alaska (6194 m; 20,320 ft) is the highest peak in North America. In the Pacific Northwest, Mt. Rainier is the highest mountain in Washingon at 4392 m (14,409 ft, Figure 1), while Mt. Hood is the highest in Oregon (3426 m; 11, 239 ft).

The North Cascades Range provides a rugged set of young mountains, geologically complex, and heavily glaciated. Mt. Baker, Glacier Peak and Mt. Rainier, high ice-covered volcanoes, are the most conspicuous mountains scattered along the crest of the Range. Below the ice, these 'island' mountains support well-developed alpine plant communities in moist and cool environments (Douglas and Bliss 1977, Billings 1989). The Cascades Range is distinguished by being one of the snowiest places on the planet. Mt. Rainier and Mt. Baker have the right combination of winter precipitation and oceanic air currents, as well as steep temperature and elevational gradients to generate impressive snowfall. During 1998-1999 winter, Mt. Baker recorded a world record snowfall of 28.9 m (95.0 ft, U.S. Department of Commerce and the National Oceanic and Atmospheric Administration, Press Release, August 3 1999).

Alpine and sub-alpine habitats are among the most undisturbed habitats remaining in the Pacific Northwest. The amount or distribution of high elevation habitat in Washington and Oregon has changed little since pre-settlement times. Alpine ecosystems, however, are sensitive to sustained and heavy use. Olympic and Mt. Rainier National Parks show significant deterioration of alpine fellfields and sub-alpine meadows caused by recreational activities, grazing, and air-borne contaminants (Houston and Stevens 1988, Rochefort and Gibbons 1992, Brace and Peterson 1999, Kirk 1999). This region has also experienced several impressive natural disturbance events. The Mt. St. Helens volcano in Washington erupted in 1980, scorching or levelling 500 km$^2$ (200 mi$^2$) of surrounding forest up to a distance of 25 km (15 mi, Frenzen and Crisafulli 1990). Recovery of the mountain flora and fauna after this natural disturbance is of special ecological interest to biologists. Shortly after Mt. St. Helens cooled, wildlife species began to recolonize and, recovery

continues. Species with the most complete recovery tend to be associated with standing dead trees, stream ecosystems, or living beneath the soil surface (Manuwal et al. 1987, Crisafulli and Hawkins 1998).

The Cascades Mountains, the major mountain range in the region, extend from British Columbia south through Washington and Oregon to California. The Selkirk Mountains run from southern British Columbia to northeastern Washington. The Olympic Mountains lie west, and the Okanogan Highlands lie east of the Cascades Range. The major mountain ranges in Oregon are the Wallowa Mountains, Blue Mountains, Steens Mountain, and the Siskiyous.

## 2. High Elevation Wildlife Habitats In Washington And Oregon

In Washington and Oregon, the two main high elevation wildlife habitats classified were Sub-alpine Parklands (#9) and Alpine Grasslands and Shrublands (#10, Kiilsgaard 1999, Chappell et al. 2001). These habitats comprise about 2.2 % of the Washington and Oregon land base (Table 1), and include a broad diversity of alpine habitats and conditions. Coastal or maritime alpine located on the western side of the mountains differs dramatically from interior mountain ranges on the eastern side (Franklin and Dyrness 1973, Billings 1989). On the western side, there is more coastal alpine, connected to Upper Aspen habitat, montane conifers such as Engelmann spruce (*Picea engelmannii*) and sub-

alpine fir (*Abies lasiocarpa*), and coniferous wetland habitat types. On the eastern side, it is drier, alpine habitats are at higher elevations, and these are connected to lodgepole pine (*Pinus contorta*) and high shrub Steppe habitat types (Cassidy et al. 1997). Locally, high elevation habitats also differ in climate, vegetation, and processes such as treeline and resilience to impacts depending upon location, slope, elevation, and aspect.

**Sub-alpine Parkland** habitats occur below alpine or krummholz (the zone where growth of trees and shrubs is stunted and deformed) and above continuous sub-alpine forest. The parklands are mosaics of patches of herbaceous or dwarf-shrub vegetation and tree islands or scattered trees with 10 to 30% canopy cover. Sub-alpine Parklands occur throughout the high mountain ranges of Washington and Oregon, extending north into Canada, and south to the Sierra Mountains. Mountain hemlock (*Tsuga mertensiana*) sub-alpine parklands occur along the Cascades Crest and in the Olympic Mountains. In the west Cascades and Olympic Mountains, Sub-alpine Parklands are mosaics of tree patches and heath shrublands or wetlands. Sub-alpine Parklands in the east Cascades and Wallowa Mountains, occurring at slightly higher elevations (up to 2438 m, 8000 ft; Table 1), contain whitebark pine (*Pinus albicaulis*) and sub-alpine fir with ground cover typically dominated by sedges and grasses, and with less heath

## Table 1. Areas of high elevation habitats, and elevational ranges for Washington and Oregon[a]

| | Washington | | | | Oregon | | | |
|---|---|---|---|---|---|---|---|---|
| | Acres | Sq. mi | km$^2$ | % Protected[b] | Acres | Sq. mi | km$^2$ | % Protected[b] |
| #9. Sub-alpine Parklands[c] | 327,442 | 512 | 1,325 | 58.2 | 84,240 | 132 | 341 | 57.5 |
| #10. Alpine Grasslands and Shrublands[d] | 1,599,115 | 2,499 | 6,471 | 81.3 | 291,494 | 455 | 1,180 | 56.0 |
| Total high elevation area | 1,926,557 | 3,010 | 7,796 | 77.4 | 395,734 | 618 | 1,601 | 56.3 |
| Total state land base | 43,164,632 | 67,443 | 174,678 | | 61,974,831 | 96,834 | 250,800 | |

[a] Kiilsgaard (1999).
[b] Percent of habitat type protected in Category 1 and 2 (Shaughnessy and O'Neil 2001).
[c] Elevation west of Cascade Crest (1372 to 1829 m; 4,500-6,000 ft), East of Cascade Crest (1524 to 2438 m; 5,000-8,000 ft).
[d] Elevation: 1524 m (5.000 ft) to > 3050 m (10.000 ft).

## Table 2. Living And Breeding In High Elevation Environments: Constraints, Consequences and Wildlife Adaptations

**A. Environmental Constraints**

- Cold and extreme temperatures
- High winds
- Open habitats
- Strong temporal resource gradient (melting snow fields)
- Strong spatial resource gradient (food phenology)
- Aridity
- UVB light
- Hypoxia
- Airborne toxins
- Fragmented habitats

**B. Ecological Consequences**

- High energetic costs for living and breeding
- Cooling and warming adaptations required
- Patchy distribution and strong seasonality of resources
- Low parasitism levels, good health
- Delayed breeding schedules
- Increased reproductive synchrony
- Increased reproductive stochasticity
- Fewer broods/litters per season
- Longer development times
- High predation risk on young and adults
- Small, low density populations
- Need to disperse across unsuitable habitats

**C. Biological Adaptations**

Physiological

- Increased visual acuity
- Large thermal neutral zone for heat and cold
- Biochemical adaptations to hypoxia
- Molting patterns for cryptic plumage
- Night-time torpor
- Flexible reproductive timing
- High tolerance for environmental toxins
- Cold-tolerant embryos, antifreeze solutions

Structural

- Larger body size
- Thicker, warmer pelage/plumage
- Appendages modified for wind stabilization

Behavioral

- Cryptic behavior
- Non-directional vocalizations
- Social and/or sub-nivean roosting
- Energy-minimizing behaviors such as gliding and walking uphill

**D. Life History Adaptations**

- Cryptic pelage/plumage
- Extensive molting patterns
- Increased parental care
- Monogamous mating system
- Strong seasonality in habitat use
- Hibernation or dispersal in winter
- Increased longevity with elevation
- Strong age dependence and senescence
- Excellent dispersal/migration abilities
- External recruitment for rescue

than found in Alpine Grasslands and Shrublands.

**Alpine Grasslands and Shrublands** include all vegetated areas above the upper treeline in the highest mountains, as well as significant expanses of grassland just below the upper treeline within the sub-alpine zone. Upper treeline is defined as the elevation above which trees are unable to grow in an upright form. Alpine vegetation is dominated by sedge species, grasses, hardy forbs and/or dwarf shrubs such as heathers. This habitat type includes the krummholz. Alpine Grasslands and Shrublands occur in the high mountains throughout the Cascades, Olympic Mountains, Okanogan Highlands, Wallowa Mountains, Blue Mountains, Steens Mountain in southeast Oregon and occasionally in the Siskiyous. Alpine heath communities are found primarily along the Cascade crest and west, especially from Mt.

## 1. Getting by on high:  Avian adaptations to high altitude and life history adjustments

Alpine and arctic birds face similar problems of living in habitats characterized by low temperatures, high winds, short growing seasons and delayed breeding schedules.  At high altitudes, hypoxia and aridity further elevate energetic costs for survival and reproduction. Physiological adaptations and life history traits of white-tailed ptarmigan in the Colorado Rocky Mountains (3600-4400 meters) are compared with arctic willow ptarmigan (0.5-800 m).  Ptarmigan embryos in the alpine must develop at cellular oxygen tension levels that are normally lethal for tissue maintenance (Carey 1980, Carey and Martin 1997). To deal with hypoxic conditions, white-tailed ptarmigan embryos have elevated levels of blood hematocrit and citrate synthase enzyme in muscle tissue at a much earlier stage of development than willow ptarmigan that show similar levels to other avian embryos at low elevations. Hematocrit and red blood cell organic phosphate levels decline when white-tailed ptarmigan clutches are incubated at lower altitudes, indicating that high elevation levels are a physiological acclimatization to hypoxia, rather than a genetic adaptation (Carey and Martin 1997, Dragon et al. 1999). Daily temperatures in the alpine range from -2 °C to >45 °C and,  females adjust incubation schedules based on nest site type and ambient temperature (Wiebe and Martin 1997). Cooling as well as generating heat to maintain homeothermy is likely a problem for most alpine vertebrates. Embryo viability does not differ between the two species, but living at high elevation likely imposes significant life history costs.  Alpine ptarmigan have smaller clutches, slower egg laying rates, longer incubation periods and higher predation than arctic ptarmigan (Martin et al. 1993). Alpine birds show stronger age-dependent effects on survival and reproduction compared to arctic ptarmigan (Wiebe and Martin 1998).

impacts. Frost heaving can have small-scale but important effects on alpine vegetative communities (Edwards 1980). Wind blasting and extreme variation in snow pack between years in high elevation habitats can kill and desiccate plants or shorten growing seasons. Because seedling establishment is generally poor, most alpine plants also propagate by clones or stolons (Körner 1999). Trees often invade from wind-dispersed seeds, but seed dispersal by mountain birds such as Clark's nutcrackers (*Nucifraga columbiana*) may determine upper treeline, especially for whitebark pine (Lanner 1988, Tomback 1998). Tree invasion rates into Sub-alpine Grasslands are slow compared to sub-alpine tree or shrub communities (Kuramoto and Bliss 1970, Franklin et al. 1988). Herbivory and associated trampling disturbance by elk (*Cervus elaphus*) and mountain goats (*Oreamnos americanus*) creates patches of open ground (Houston and Stevens 1988). Avalanches and snow-slumping convert coniferous forest to open meadows or deciduous forests providing nutritious forage for breeding or migrating birds, rodents, bears, and ungulates (Krajick 1998). Sub-alpine grasslands burn on occasion, but since 80-90% of sub-alpine plant biomass is underground, fire does not affect the structure of sub-alpine grasslands greatly. In Sub-alpine Parklands, fire suppression has contributed to changes in habitat structure and function. During wet climatic cycles, reduced fire frequency can lead to tree islands coalescing and, parklands becoming a more closed forest (Agee and Smith 1984). Area of alpine grassland, however, may be increased by fires in Sub-alpine Parklands (Kuramoto and Bliss 1970). Periodic shifts in climatic factors such as drought, and depth or duration of snow pack may either lower treeline or allow tree invasions into meadows and shrublands creating more parkland habitat.

**Status and trends**: There has been little change in abundance of alpine habitat over the past 150 years. Most areas are dominated by native species and are still in good condition (Kiilsgaard 1999). Current trends for most alpine grasslands are considered stable, but there are increasing threats from recreational pressures and livestock grazing, and possibly some slow loss of sub-alpine grassland to recent tree invasion. Conditions are changing, however, as over the past half century, mountain recreational activities have increased markedly. Some alpine areas on the eastside are degraded physically. Recreational impacts are noticeable in some national parks and wilderness areas. Mt. Rainier National Park gets two million visitors per year, most of whom converge on Paradise and Sunrise sub-alpine meadows. Sedge turfs are the most resilient to trampling and heaths the least resilient. When alpine heath is opened up to bare ground it typically does

Rainier north. Sub-alpine and alpine wetland habitat occurs throughout the range, and is more common in the high mountain ranges of Washington (Cassidy et al. 1997).

Most natural disturbances in Alpine Grasslands and Sub-alpine Parklands involve weather events or animal activities, and usually have small-scale

not revegetate for decades unless active restoration programs are initiated. Sunrise Meadow in Mt. Rainier National Park has had success in restoration of the sub-alpine meadows (Rochefort and Gibbons 1992, Kirk 1999). The major human impacts to high alpine grasslands are trampling and associated impacts caused by tent sites on Mt. Rainier National Park (Kirk 1999). Exotic ungulates, such as the mountain goats introduced to the Olympic Mountains, can have profound impacts on high elevation grasslands (Houston and Stevens 1988). Grazing by domestic animals also has negative impacts (Braun et al. 1976), but these effects are not well studied in the Pacific Northwest. Sub-alpine Parkland habitat trends are believed to be generally stable. Whitebark pine may be declining due to effects of blister rust or fire suppression (Kuramoto and Bliss 1970). For Alpine Grasslands and Shrublands, only one of 40 plant associations listed in the National Vegetation Classification is considered threatened, and less than 10% of the Pacific Northwest Sub-alpine Parkland community types are identified as threatened (Grossman et al. 1998).

### 3. Alpine Environments and Wildlife Adaptations for High Altitudes

Alpine environments are characterized by low mean temperatures, high winds, prolonged snow cover, and intense ultraviolet radiation (Billings and Mooney 1968, Table 2A). Topography varies from steep to gentle, and winter snow pack ranges from several meters in gullies to exposed windswept ridges. Although the vegetation structure is simple, variation in slope and aspect results in rapid changes in habitat types with only modest changes in elevation, thus generating significant structural complexity to alpine habitats. Steep local gradients in snow cover and soil moisture often govern the productivity and distribution of alpine plants (Billings 1989). Precipitation is more important than temperature for alpine plant growth, as most plant species are cold tolerant and can carry on photosynthesis down to -6 °C (Billings and Mooney 1968).

Wildlife living at high elevations must be able to cope with high winds, cold temperatures and desiccation, since often little precipitation originates from rainfall and it drains quickly. Although alpine soils are normally cold, daily temperatures on the ground vary over a range of 47 °C (Wiebe and Martin 1997, Box 1). Thus, during mid day, overheating can be a problem for alpine wildlife species. On elevational gradients, resources can be patchily distributed in narrow bands of diverse habitat types that vary sharply in time within a season (e.g., plant phenology or insect emergence; Table 2B). Spatial

and temporal variation in resources can extend the availability of food and cover to wildlife, but also requires good mobility and longer migration distances from patchy breeding habitats to winter areas. Alpine environments also show significant stochasticity in environmental conditions annually. Some years have low snow cover leading to an absence of cover for sub-nivean species and, in other years, like 1999 in the Pacific Northwest, much breeding habitat remained snow-covered for the entire season (K. Martin unpubl. data). At the highest elevations, hypoxic conditions add an additional energy cost (Bullard 1972, Martin et al. 1993). These factors result in short, intense breeding seasons for wildlife.

Animals respond to living in extreme environments in several ways. They can migrate to warmer environments, hibernate or stay active all year. Alpine animals that stay active all year have developed biological and life history adaptations to survive in these extreme habitats (Table 2). Vertebrate species living at high elevations have developed impressive physiological, behavioral and morphological adaptations to conserve energy (Table 2C). The type of adaptation may increase with elevation, or with increased time spent at high elevation. For example, species that use low elevation alpine or high alpine for only short periods may require only behavioral adjustments like moving to more benign or sheltered sites to conserve energy (Cody 1985, Landmann and Winding 1995b). Hummingbirds exploiting the rich resources in sub-alpine meadows during migration go into nighttime topor if their energy reserves at nightfall are below a critical setpoint (Carpenter and Hixon 1988). With less vegetative cover for concealment, many alpine mammals and birds have developed cryptic appearances and behaviors to enhance blending into the landscape. Although ptarmigan are renowned for their cryptic plumage, larger mammals such as bighorn sheep (*Ovis canadensis*) and coyotes (*Canis latrans*) blend exceptionally well in these open landscapes. Often species living in the alpine such as marmots, pika and ptarmigan have territorial and social contact calls that are hard to localize, which may reduce risk of detection by predators when vocalizing (Braun et al. 1993). Like arctic wildlife, animals living at high elevations develop fat deposits, extra feathers or thicker fur to increase insulation. Red foxes (*Vulpes vulpes*) in the alpine develop a thick pelage and a faded cryptic gray coat color.

True alpine species may develop structural adaptations. Species living at the highest elevations for extended periods make biochemical adjustments such as increasing their blood haematocrit concentrations (Box 1, Bullard 1972, Carey 1980,

Carey and Martin 1997). In the Himalayas, alpine passerines tend to have long pointed wings for efficient flight to scattered resources and improved flight performance in strong and variable winds. Finches and chats at the highest elevations have square-ended or only shallow forked tails for flight stability in wind, and strong hind limbs with small feet for ground foraging (Landmann and Winding 1993; 1995 a and b). Winds may pose problems for smaller animals, but larger animals such as raptors use wind to remain aloft and move efficiently.

The reduced time for breeding within a season may alter life history traits. Generally, vertebrate species living at high elevations exhibit lifestyles where it takes longer to achieve independence, there is lower expected annual fecundity and, at least for some species, accompanied by longer life spans and more developed social behaviors. White-tailed ptarmigan (*Lagopus leucurus*), a high alpine grouse, showed slower laying rates, smaller clutches, longer incubation periods with consequent higher reproductive failure compared to arctic breeding willow ptarmigan (*L. lagopus*; Martin et al. 1993, Box 1). A study of golden-mantled ground squirrels (*Spermophilus lateralis*) across five elevations in the Sierra Nevada in California showed reduced time above ground for adults and juveniles, later age of maturity, lower litter size and greater survivorship of females with increasing elevation (Bronson 1979). Parental care patterns vary with elevation in marmots. Alpine marmots (*Marmota marmota)* have prolonged parental care, live and hibernate in larger groups and take longer to reach maturity compared to marmot species living at lower elevations (Arnold 1990 a and b, 1993, Armitage 1999, Box 2).

Among mountain ungulates, there is considerable variation in patterns of parental investment and time to offspring independence in high and low elevation populations, but it is not clear what influence alpine habitats have in explaining these patterns. In order to maximize maternal survival, mountain goats may reduce their investment in reproduction with increasing altitude, but species spending more time at high elevations may prolong the period of maternal care to young (Festa-Bianchet et al. 1994, Gaillard et al. 1998). Delayed primiparity may be the life history trait most likely to vary with elevation for ungulates (M. Festa-Bianchet, pers. comm.). One expects other life history tactics such as increased probability of bet hedging against the regular but stochastic reproductive failure (Bronson 1979), but such demographic parameters are usually not available for species living at high elevation.

Despite the tendency for small population sizes, birds adapted to live in naturally fragmented alpine habitats appear to have well developed dispersal abilities (Box 3). Pikas also are excellent dispersers (Smith 1974), but generally dispersal from and to alpine habitats is more challenging for alpine mammals than birds. The frequent speciation of high elevation marmots (Olympic (*Marmota. olympus*), Hoary (*M. caligata*), Yellow-bellied (*M. flaviventris*), and Vancouver Island (*M. vancouverensis*)) and ground squirrels (Beldings, Columbian, golden-mantled and Cascade golden-mantled) may have been in response to isolation imposed by dispersal barriers.

## 4.  Advantages to Living and Breeding in Alpine Habitats

Why would any animal live at high elevation given the extreme environmental conditions and the high energetic costs to living there? Is it worth it? The answer is that there are definite advantages to living in high elevation environments. In winter, despite extensive snow pack, most alpine areas have wind-swept ridges with exposed herbaceous stems and seeds for foraging, and as winter progresses, increasing snow levels allow herbivores access to new layers of vegetation. In spring, vast numbers of cold-numbed insects are swept up from lower elevations to land on high elevation snow fields. These insects provide a nutritious and abundant food supply for alpine-breeding birds and mammals (Spalding 1979, Norvell and Creighton 1990). Snowfields melting through the season create a gradient in plant phenology that provides an extended supply of high quality food for herbivores that can migrate along the green-up line. In late summer, leaf budding, flowering and fruiting of huckleberry (*Vaccinium deliciosum*) or bearberry (*Arctostaphylos uva-ursi*) may co-occur in close proximity grading away from the edge of a snowfield. Avalanche chutes at high elevation provide lush vegetation adjacent to forest cover for bears, marmots and songbirds. Availability of spring forage may be crucial for breeding in a number of species such as bighorn sheep and mountain goats (Festa-Bianchet et al. 1994, Portier et al. 1998). Generally, compared to other habitats, there are few intraspecific or interspecific competitors relative to food supplies.

Predation risk in the alpine may or may not differ from lower elevation sites, but it appears easier for prey to detect aerial and mammalian predators in open alpine habitats. It is a challenge for medium and large predators such as foxes, mountain lion (*Felis concolor*) and wolves (*Canis lupus*) to approach prey undetected, although they are clearly successful in doing so. In northern British Columbia, caribou (*Rangifer tarandus*) give birth to their calves at alpine sites because they are considered to be refugia

## 2. Sleeping through winter with family members: Marmot hibernation and sociality

Marmots are large diurnal, ground dwelling rodents that occupy middle and upper elevation alpine and sub-alpine mountains across North America and Eurasia. At the high elevations in Washington and Oregon, the three marmot species living in alpine and sub-alpine habitats have non-overlapping ranges. Yellow-bellied marmots occur in habitats # 9 and #10 only in Oregon, and in Washington are replaced in the high elevation habitats by hoary marmots, which live only in the Cascades. The Olympic marmot is restricted to the Olympic Peninsula. Marmots are the largest true mammalian hibernator, with species spending from 4.5 to 8.5 months per year underground (Armitage 1999). Marmots thus, have a short active season above ground, on average 4.8 months, when they must grow, reproduce, and prepare for hibernation. Marmots have complex social systems, delayed maturity of young, and flexible patterns of dispersal and recruitment as a consequence of their large body size and living in extreme and patchy environments (Arnold 1990 a and b, Armitage 1999). The degree of sociality across the 14 marmot species correlates with environmental harshness and increases with altitude and latitude (Arnold 1993). The low elevation woodchuck (*Marmota monax*) is solitary, young of the year disperse from natal burrows, and individuals usually reproduce after their first hibernation (Ferron and Ouellet 1989). The yellow-bellied marmot, the smallest marmot, lives at medium to high altitudes (Frase and Hoffman 1980) and is moderately social. The basic social units are polygynous groups usually developed through recruitment of daughters. Dispersal of young typically occurs after the first hibernation (Armitage 1999). European alpine marmots (*M. marmota*), living at the highest elevations, are the most social species with up to 20 individuals in a group defended by a dominant male and female (Arnold 1993). Juveniles typically do not disperse for two or more years, and their over-winter survival is enhanced by increased group size in joint hibernacula (Arnold 1990 a and b, 1993). Like birds, the principle life history costs incurred by marmots living in alpine and sub-alpine environments appear to be time delays. Young require more (longer) parental care at higher elevations and thus remain with their parents or extended family for one or more years after they reach maturity (Arnold 1993, Armitage 1999). Delayed dispersal results in groups of high relatedness, which in some species leads to reproductive suppression of subordinate members in the group (Armitage 1999). Reproductive skipping between years occurs in hoary and Olympic marmots due to extreme conditions, but not in yellow-bellied marmots (Armitage 1999). Higher longevity is observed in high elevation marmots, and this may be due to delayed dispersal, reproductive skipping, or higher sociality that may reduce predation risk (Armitage 1999).

from predators (Shackleton 1999), and possibly also from biting insects.

Alpine habitats appear to be healthy environments with low levels of parasitism or disease, at least for alpine grouse, which have few blood infections or intestinal parasites (Stabler et al. 1974, Braun et al. 1993). Blood parasite infections in white-tailed ptarmigan varied with degree of fragmentation in the low elevation coastal alpine on Vancouver Island as 84% of 25 birds sampled on isolated mountains in the north and south had blood parasites compared to only 57% of 53 individuals in the more continuous alpine in Strathcona Provincial Park (K. Martin and N.J.K. Braun, unpubl. data). The higher rates on smaller, more isolated mountains were likely related to ptarmigan mixing more with blue grouse (*Dendragopus obscurus*) at these sites. In contrast to birds, parasites and infectious viruses can be a problem for alpine marmots (Arnold 1993), and other mammals. Alpine ungulates, particularly bighorn sheep, are susceptible to a range of infectious diseases including pneumonia and blood and organ parasites, especially when animals are in contact with domestic livestock (Onderka et al. 1988, Foreyt et al. 1994, Pybus et al. 1996).

Relative to the arctic where long distance migrations to winter sites are required for most seasonal breeding species, winter habitat for alpine species often occurs in close proximity to breeding sites. In alpine habitats in the Pacific Northwest, animals may simply descend one or a few kilometers to habitats that offer greater shelter or more benign weather. In the low elevation coastal alpine in central Vancouver Island, white-tailed ptarmigan moved around the mountain to a southern or western aspect to winter in openings in the montane forest or parkland only 100 to 400 m (300-1000 ft) lower in elevation than their breeding habitat. In the Cascades Range, ptarmigan likely make similar movements in winter.

### 3. Patterns and mechanisms of rescue and dispersal in alpine ptarmigan

The periodic 'rescue' of populations that are declining with recruitment from productive populations may be an important feature of population biology for many species. Dispersal and recruitment are crucial life history parameters for persistence of populations or metapopulations, but data on patterns and mechanisms are lacking for most vertebrates. We studied four populations of white-tailed ptarmigan (*Lagopus leucurus*) breeding in highly fragmented alpine habitats, with corresponding small populations, in the Rocky Mountains of Colorado, from 1987 to 1996. Multiple populations allowed us to distinguish between local and regional events. Populations showed dramatic variation in offspring production and local survival (return) of adults across years and sites, yet populations remained relatively stable. Variation in reproductive success and survival were unlinked across sites and appeared to be driven mainly by internal ecological processes such as depredation of eggs and young (Braun et al. 1993). Sites varied temporally in predation risk (Braun et al. 1993), perhaps because the generalist predators that prey on ptarmigan live for several years and their hunting skills likely improve with age. Computer simulation models of individual populations predicted that all populations should go extinct in 2 to 10 years, assuming no linkage between them. Treating the four populations as different fragments of a single large closed population resulted in predicted persistence times of about nine years (Martin et al. 1997). Yet all populations have persisted for at least 30 years and likely substantially longer. In one site, the population remained stable despite zero production the previous year and no return of breeding females.

Ptarmigan have adapted to breeding in highly fragmented and stochastic alpine habitats with a system of extensive external recruitment that functions at a landscape scale. Local populations were able to avoid extinction due to external recruitment since about 95% of females and 75% of males recruiting to sites did not originate from any of the studied populations. Excellent dispersal abilities allowed recruitment from populations during a productive episode to rescue populations at risk of collapse were they dependent solely on internal recruitment. Studies of radio-marked juveniles in Colorado revealed a spatial scale of about 35 km (22 mi), and movement patterns of juveniles were not related to locations or movements of their mothers (Martin et al. 2000). The enabling factors for this extensive external recruitment appear to be low costs to dispersal and low benefits to philopatry. Observations and experiments on mate and territory replacement showed no apparent reproductive costs to females that switch mates or territories (Hannon and Martin 1996, K. Martin unpubl. data), suggesting that dispersal to unfamiliar sites is not costly. Populations will be maintained as long as there is a balance of populations producing recruits in reasonable proximity to populations requiring rescue. Rescue by external recruitment appears to apply to other grouse such as red grouse (*Lagopus lagopus scoticus*), sage grouse (*Centrocercus urophasianus*) and capercaillie (*Tetrao urogallus*) (Storch 1997, Piertney et al. 1998), and perhaps generally to other taxonomic groups. For small populations in stochastic environments, maintaining connectivity between populations is crucial because populations producing recruits must be within reasonable proximity to those requiring rescue (Martin et al. 2000).

Despite their reputation for unfavorable thermal conditions, alpine habitats offer thermal advantages for wildlife species in both winter and summer. Winter is reliably cold, usually remaining below freezing for periods of seven to eight months. Thus arousal for hibernating animals is likely to occur at appropriate times. There is generally a reliable supply of snow to provide well-insulated and safe sub-nivean habitats. Summers are reliably cool and breezy and a number of birds and mammals escape the late summer heat and insects at lower elevations by moving up to alpine meadows to forage. Temperature inversions are common in mountain landscapes and, provide an exception to the general rule of decreased temperature with increased elevation. A thermal belt results in warmer temperatures at mid-slope than either the valley bottom or the upper slopes (Price 1981). On the north slope of Mt. Hood in Oregon, a sharply delimited thermal belt between the Hood River valley bottom and the upper slopes allows suitable growing conditions for such crops as cherries.

In winter, thermal inversions occur in high elevation areas, and temperatures may remain high for several weeks. In the Northeastern Asian highlands, temperatures at timberline from December to February can be 25-30°C warmer than the low forest conditions of -50°C. Moose (*Alces alces*) migrate to high elevation habitats during thermal inversions, possibly to capitalize on the favorable temperatures, although they may also be attracted to sub-alpine shrublands (A. Andreev, pers. comm.).

In summary, there may be high ecological costs to living in open habitats at high elevations as the need to move for food or cover may result in increased risk of detection by predators. However,

alpine animals likely experience lower levels of interspecific competition and less habitat degradation than wildlife occupying lower elevation habitat types.

## 5. Resident Wildlife and Migrant Visitors to Alpine and Sub-alpine Habitats

**Year-round and summer residents.** Only a few North American bird species, white-tailed ptarmigan, American pipit (*Anthus rubescens*), black-crowned rosy finch (*Leucosticte atrata*), gray-crowned rosy finch (*L. tephrocotis*), the alpine sub-species of horned lark (*Eremophila alpestris alpinus*), and golden-crowned sparrow (*Zonotrichia atricapilla*) breed exclusively in alpine and sub-alpine habitats. Of these, only ptarmigan are year-round residents (Figure 2, 3). Mammals, such as hoary marmots, Olympic marmots, Cascade golden-mantled ground squirrel (*Spermophilus saturatus*), mountain goat, pika (*Ochotona princeps*) and water vole (*Microtus richardsoni*), associate primarily with high elevation habitats year-round. Pika can live at low elevations if appropriate habitat features occur, such as talus, but high elevation populations are non-migratory. Overall, more species of mammals are closely associated with high alpine habitats than birds (Table 3). There are no true alpine amphibians or reptiles in the Pacific Northwest, and only the Cascade frog (*Rana cascadae*) is closely associated with sub-alpine parkland habitats (Table 3).

Alpine songbirds face special challenges to survive and breed in alpine environments. With their small body size they must cope with cold temperatures and high winds as well as incubate small eggs that cool rapidly in near freezing ambient temperatures. All alpine and sub-alpine passerines provide bi-parental care to their altricial young. True alpine passerines (birds breeding only at high elevations) are hardy and appear to survive well despite storms and inclement weather. They take shelter from wind beside or under rocks, and sit on dark rocks to warm up in cold sunny weather (K. Martin, unpubl. obs.). A study of alpine finches showed ecological and morphological differentiation across an elevational gradient in the Himalayas with the heaviest species occupying the highest elevations (Landmann and Winding 1993; 1995 a, b). Both sexes of the alpine sub-species of horned lark, which lives only in the Washington Cascades and Olympic Mountains, have longer wings and tarsus than low elevation sub-species in the same region (*in* Beason 1995).

Most alpine passerines are both granivorous and insectivorous (Verbeek 1981). Within alpine sites, species tend to use different micro-habitats and foraging modes. Rosy finches, associated with steep rocky slopes, are slow searchers for insects and seeds, while horned larks and pipits are active searchers in more grassy areas (Cody 1985). Wheatears (*Oenanthe oenanthe*) frequent open slopes and plains and pounce from boulder perches to capture ground and low flying insects. Food supplies in alpine sites for songbirds are plentiful generally, but of short duration (Cody 1985). Receding snow fields in summer continually uncover new food for rosy finches and pipits (Twining 1940). Many alpine passerines forage on chilled and dead wind-blown arthropods deposited on snowfields (Spalding 1979). Verbeek (1970) emphasized the importance of having snowfields to provide an insect food supply within territories of pipits in Wyoming. However, horned larks and pipits foraged more frequently in snow free areas than on snow on Mt. Baker in Snoqualmie National Forest, although both species did use snowfields in late afternoon after updrafts from low elevations deposited insects on snow (Norvell and Creighton 1990). The proportion of energy budget provided by chilled insects on snowfields was not determined in any of these studies.

With such limited vertical structure in the alpine, passerines need to choose nest sites that are protected



*Fig. 2. White-tailed ptarmigan in winter plumage and in winter habitat at Guanella Pass, Colorado with Mount Evans (breeding habitat) in the background. Photo by K. Martin, January 1998.*

*Fig. 3. Male (l) and female (r) white-tailed ptarmigan in cryptic spring breeding plumage feeding on alpine territory, Loveland Pass, Colorado. Photo by Robert E. Bennetts.*

as much as possible from predators and extremes of wind, precipitation, or temperature. Rosy finches and mountain bluebirds (*Sialia currucoides*) nest in inaccessible cliffs or rock crevices, while pipits and horned larks nest on open grassy tundra slopes that are potentially more exposed to predators and climatic extremes. Johnson (1965) reported 81% of 139 rosy finch nests were in cliff crevices, and suggested that rodents might limit rosy finch nesting to cliffs. Nest sites in cliff crevices and under rocks are colder thermal environments than open cup nest sites in the alpine and arctic tundra (Lyon and Montgomerie 1987, Wiebe and Martin 1997). Water pipits (*Anthus spinoletta*) in Austria spent three to

four weeks choosing potential nest sites within their territories (Böhn and Landmann 1995). Nest sites were on steep slopes and oriented NW-NE providing shelter from drifting snow or rain. All nests were placed below ground level with a solid nest roof resembling a nest cavity more than a nest cup and providing considerable insulation against the cold alpine temperatures (Verbeek 1981, Böhn and Landmann 1995). American pipit nests are sunk into the ground on steep grassy slopes (Verbeek 1970, Medin 1987).

The breeding schedules of alpine bird species are three to six weeks later than those for related species at low elevations. Initiation of egg-laying in white-

## Table 3. Vertebrate species use of sub-alpine and alpine habitats in Washington and Oregon[1]

|  | Mammals | | | | Birds | | | | Herptiles | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | A[2] | B | C | D | A | B | C | D | A | B | C | D |
| Sub-alpine parklands (#9) | 11 | 39 | 15 | 65 | 7 | 48 | 47 | 102 | 1 | 7 | 3 | 11 |
| Alpine grasslands (#10) | 13 | 22 | 14 | 49 | 5 | 16 | 52 | 73 | 0 | 4 | 1 | 5 |
| Number of Species |  |  |  | 65 |  |  |  | 112 |  |  |  | 11 |

[1] Associations derived from Expert Panels of the Species Habitat Project and supplemented by data from Washington (Smith et al. 1997), Oregon (Csuti et al. 1997), British Columbia (Campbell et al. 1990, 1996), and Colorado (C. E. Braun 1969), as well as unpubl. data from K. Martin (University of British Columbia—http://www.forestry.ubc.ca/alpine/index.htm), and field counts from L. Steiner, Washington.

[2] A = Closely Associated; B = Associated; C = Present; D = Total.

tailed ptarmigan populations above 3200 m (10,500 ft) in Colorado may begin on 25 May and extend to 11 July (mean of 8 June; 5 years; Braun et al. 1993), about six weeks later than ruffed grouse, a low elevation ground nesting tetraonid, that commences egg laying by 10 April and extends to 19 July in British Columbia (Campbell et al. 1990). Some alpine species extend breeding later into the season to compensate for their late start in spring. There was no overlap in laying dates for rosy finches in the Montana Rocky Mountains (egg laying 16 June to 6 July), over seven weeks later than on Amchitka Island, Alaska (28 April to 26 May; Johnson 1983). The alpine sub-species of horned lark at 3200 m in Wyoming laid eggs between 25 June and 10 July, up to three months later than low elevation populations (Verbeek 1967, Beason 1995).

Some mountain goat and bighorn sheep herds remain at high elevation year-round, subsisting in winter on the windswept alpine grasslands and meadows. Herds consist of small groups of bachelors or female with young. Mountain goat populations may be limited by quality and quantity of winter food as suggested by Houston and Stevens (1988), but recent work indicates that spring weather or timing of access to new plant growth in spring is more important than winter conditions (Portier et al. 1998, M. Festa-Bianchet, pers. comm.).

**Species breeding across wide elevational gradients.** Some birds and mammals range naturally across wide elevational gradients with their breeding habitats sometimes extending from coastline into the alpine zone (Table 3). Allee and Schmidt (1951) referred to this group as 'alpine-tolerant'. Examples include Canada geese (*Branta canadensis*), blue grouse, rufous hummingbird (*Selasphorus rufus*), killdeer (*Charadrius vociferus*), dipper (*Cinclus mexicanus*), mountain bluebird, rock wren (*Salpinctes obsoletus*), and Townsend's solitaire (*Myadestes townsendi*), and a variety of mammals such as long-legged Myotis bat (*Myotis volans*), white-tailed jackrabbit (*Lepus townsendii*), yellow-bellied marmot, Beldings (*Spermophilus beldingi*) and Columbian ground squirrels (*S. columbianus*), northern pocket gopher (*Thomomys talpoides*), western jumping mouse (*Zapus princeps*), heather vole (*Phenacomys intermedius*), long-tailed vole (*Microtus longicaudus*), fox, coyote, black bear (*Ursus americanus*), grizzly bear (*U. arctos*), wolverine (*Gulo gulo*), mountain lion, and big horn sheep. At high elevations, Columbian ground squirrels have lower litter size, lower female body weight, lower proportion of young females breeding, and higher adult survival relative to low elevation populations (Dobson et al. 1986). Some within-

species differences in ground squirrel life history with elevation, such as litter size and proportion of young females with litters, disappeared when high elevation populations were food-supplemented (Dobson and Murie 1987). They suggested that ground squirrel populations showed a phenotypically plastic life history response to variation in food availability with elevation. American pika range from high alpine to sea level where there are grasses and forbs close to talus. Pika show similar life history patterns to Columbian ground squirrels as high alpine populations have smaller litters and greater longevity of adults than those in low elevation talus (Smith 1974, 1978).

There are few directed studies for 'alpine tolerant' birds on whether and how life history or behavior shifts with increasing elevation. However, we can make some inferences. Breeding schedules such as arrival dates and initiation of breeding are significantly later with increases in elevation. Garden warblers (*Sylvia borin*) breeding in Switzerland at 1500 m (4921 ft) arrived on territories about three weeks later than birds breeding at 200 m (656 ft, Widmer 1996). The high elevation population of garden warblers did not extend their egg laying period beyond lower elevation populations and thus, had one or two fewer broods in a season than low elevation pairs (Widmer 1993). If restricted gene flow results in local adaptation, clutch size and/or offspring survival is predicted to be higher in high elevation environments to compensate for reduced number of breeding attempts per season. However, clutch size did not increase with elevation in garden warblers (Widmer 1993). Despite less favorable thermal conditions, both incubation and nestling periods were one day shorter in high elevation garden warblers compared to lowland populations; this was attributed to higher levels of male parental care and thicker nests (Widmer 1993). Nest structures in the high elevation population weighed almost twice as much as those at 200 m and, presumably conferred greater insulative warmth. Success of individual nesting attempts was good, but the frequency of total failure for a season was higher at increased elevation (Widmer 1993).

For most 'alpine tolerant' species, fewer broods per season are produced at higher elevations. For example, American robins (*Turdus migratorius*) breeding at low elevation in British Columbia can produce up to five clutches and three broods (Campbell et al. 1996, J.N.M. Smith, pers. comm.), but in the sub-alpine they may only have time to produce one brood, or possibly two clutches. Dippers and horned larks also produce multiple broods per season at low elevations and single broods at high elevations (Verbeek 1967, Kingery 1996).

## 4. Elevational migration: Use of high elevation habitats in late summer

Studies in British Columbia suggest that alpine areas support a high diversity and abundance of birds and mammals during late summer and fall. Since 1996, information was collected on temporal and spatial patterns of use of high elevation habitats by wildlife, especially migrating birds, on Vancouver Island and mainland British Columbia (K. Martin, University of British Columbia and Environment Canada). In 1996 and 1997, we collected data opportunistically on species use while censusing ptarmigan on 25 mountains across Vancouver Island, including relatively contiguous alpine in the central Island and more fragmented alpine habitats to the north and south. During this time, we observed 53 avian species with peak migration in these coastal alpine and sub-alpine habitats starting in late August and remaining high through September (Data summaries available on Centre for Alpine Studies web site: http://www.forestry.ubc.ca/alpine/index.htm). Only 11 (21%) of these species regularly breed in high elevation habitats (Campbell et al. 1990, 1996; Taylor 1994).

In 1998 and 1999, we surveyed alpine, sub-alpine and upper montane parkland habitats in mainland British Columbia ranging from 58° N

latitude to the Washington border. We recorded a total of 107 species and 8969 detections, using line transect sampling, over a total of 82 km (51 mi) in alpine habitat, 69 km (43 mi) in sub-alpine, and 52 km (32.3 mi) in montane parkland (approximately 270 survey hours on 62 days, years pooled). Species richness was similar in all three habitats in 1998, a warm and relatively dry summer (Fig. 4). Species richness was much reduced in 1999, a cold, wet summer with greatly delayed snowmelt and early onset of winter conditions. Except during peak migration (5-19 September), proportionately fewer species used alpine habitats than either the sub-alpine or montane in 1999 (Figure 4). In 1999, one interior site that was snow-free by late June had the greatest number of species (9 more species than in 1998). One coastal site, where the snow-line extended down to 1100 m (3610 ft) in late August, had only 26 detections/km surveyed in 1999, compared to 93 detections/km in 1998. Overall, during a 10 week period in late summer, 113 species from a diverse array of avian families used coastal and interior high elevation habitats on Vancouver Island and the central and southern mainland British Columbia. Data summaries are available on the Centre for Alpine Studies web site.
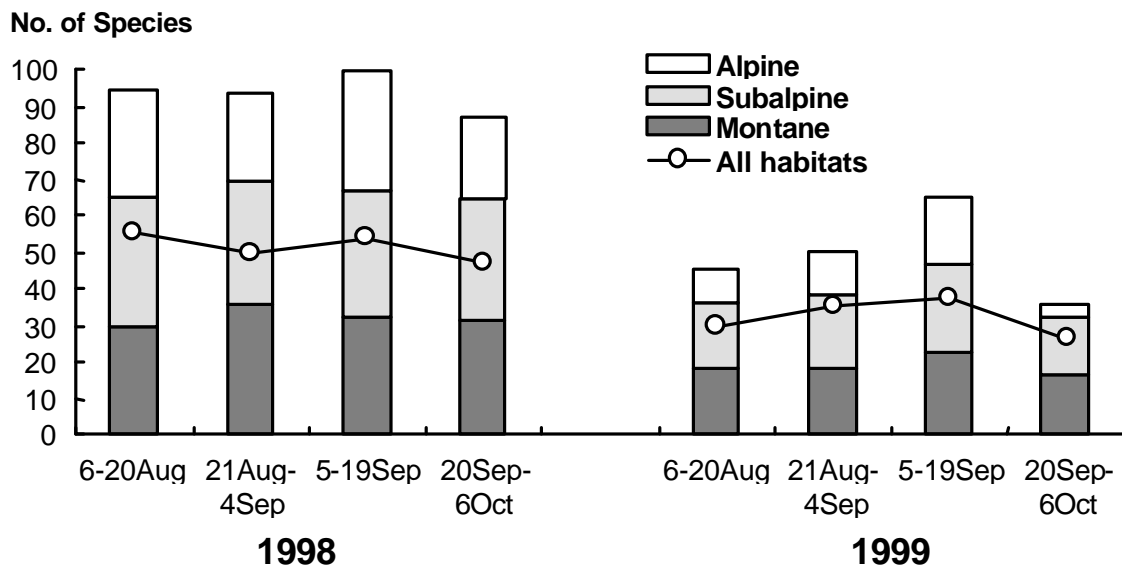


*Fig. 4. Avian use of high elevation habitats during migration in south and central British Columbia. Ten mountains were surveyed in 1998, and five sites were re-censused in 1999. Bars represent total numbers of species observed by habitat type for 10-day intervals.*

*Since many species were observed in more than one of alpine, sub-alpine or montane parkland habitats, lines represent the total species counted during each period.*

**Table 4. Characteristics of alpine and sub-alpine habitats in late summer for migrants and residents**

1. Rich food resource gradients - plants, insects and small prey
2. Open habitats to detect predators
3. Energetically more favorable for ascent (updrafts)
4. Habitat features similar to high latitude environments

Population densities of species that breed across a range of elevations are expected to decrease with increasing elevation, but this was not found for garden warblers (Widmer 1996). Densities of territorial male black redstarts (*Phoenicuros ochruros*) in Austria increased with elevation (Kollinsky and Landmann 1996). Densities of alpine chats also remained high with increasing elevation in the Himalayas (Landmann and Windmann 1993). However, these studies had small study plots and reported densities might be inflated as a result of plots being located in optimal habitats. Across elevational gradients, individuals inhabiting higher elevations were not younger or less competitive birds unable to obtain good territories at lower elevations. High elevation populations of garden warblers in Switzerland and redstarts in Austria did not contain a higher than average proportion of first time breeders, and natal philopatry and breeding site fidelity of birds in the upper elevations was high (Kollinsky and Landmann 1996, Widmer 1999).

Poikilothermic (cold-blooded) animals such as frogs, salamanders and snakes have special problems moving and developing eggs in cold alpine climates as low temperatures result in prolonged development times for amphibians and reptiles. In alpine habitats, frogs commonly pass the first winter as tadpoles and require an extra year to achieve full development (Allee and Schmidt 1951), in contrast to lower elevation individuals that usually achieve full maturity in their first year. In the Alps, the three species of reptiles, green lizard (*Lacerta vivipara*), common viper (*Vipera berus*) and blind-worm (*Anguis fragilis*) that reach the alpine zone are all viviparous (bear live young, Allee and Schmidt 1951). Reptile eggs can not develop and hatch in such cold climates, but when viviparous female snakes or lizards at high elevations retain eggs in their body, they can speed embryonic development by basking in the sun during the day, and moving to sheltered locations at night (Hesse et al. 1951, Price 1981). Interestingly, the green lizard is oviparous (egg laying) throughout most of its lower elevational

range in Europe. Snakes in the European Alps show delayed sexual maturity and reproduce only every two to four years in the alpine, rather than annually as in low elevation populations (Capula et al. 1992, Saint Girons 1992). Cold-blooded animals living in mountain environments, including amphibians, reptiles and invertebrates are almost universally dark-colored. Melanism apparently contributes to heat absorption and helps protect against ultraviolet radiation (Allee and Schmidt 1951, Price 1981). For hibernation, cold-blooded animals move under rocks or into animal burrows. They tend to aggregate in multi-species groups (insects, snakes, and lizards), and one can find predators and prey congregated under one rock for winter hibernation (Price 1981).

In Washington and Oregon, five species of amphibians and reptiles occur in alpine grasslands and 11 species of salamanders, frogs, toads and garter snakes live in sub-alpine parklands if appropriate habitat features such as standing water are available. Western toads (*Bufo boreas*) and Pacific Treefrogs (*Pseudacris regilla*) breed in high elevation ponds (Corkran and Thoms 1996). Western toads occur at elevations up to 2255 m (7,400 ft, Corkran and Thoms 1996) in Washington, and in Colorado to 3658 m (12,000 ft, C.E. Braun, pers. comm.). Garter snakes (*Thamnophis sirtalis*) occur in the alpine and sub-alpine on southern and central Vancouver Island at elevations ranging from 1540 to 1800 m (5,056 to 5,904 ft, K. Martin, unpubl. data). Little is known about the reproductive success and specific adaptations for amphibians and reptiles living in alpine and sub-alpine habitats in the Pacific Northwest.

In sum, the ecology, behavior, and life history of the upper elevational ranges for 'alpine tolerant' vertebrates is poorly understood. Quite possibly there is more restricted gene flow and greater local adaptation than we realize. Other species, in addition to horned lark, marmots and ground squirrels, may have well differentiated high elevation subspecies or ecotypes yet to be discovered. We can not calculate relative reproductive success and survival for wildlife species living at high and low elevations, mainly because longitudinal studies of individuals at high elevation sites have not been done.

**Seasonal migration of wildlife to high elevation habitats.** The seasonal migration of vertebrates to alpine and sub-alpine habitats has been noted (e.g., Pattie and Verbeek 1966, Price 1981), and naturalists acknowledge the use of alpine habitats by migrating birds (e.g., Cannings and Cannings 1996). Mammalian wildlife also move up to high elevations seasonally. However, the importance of the phenomenon is not widely acknowledged and the

ecological processes involved have not been determined. At Chinook Pass and Lake Valhalla, north of Stevens Pass in the Cascades Mountains, Washington, 32 bird species were observed during eight surveys in July, September and October (Les Steiner, unpubl. data). During field studies in central and southern British Columbia, over 113 bird species were recorded foraging or resting in high elevation habitats over a three month period (Figure 4, Box 4). About 80% of these bird species observed in late summer do not breed at high elevation. Some species were clearly migrants from higher latitudes using alpine sites as migration corridors including arctic shorebirds like Baird's sandpipers (*Calidris bairdii*) and greater yellowlegs (*Tringa melanoleuca*), and northern raptors such as sharp-shinned hawks (*Accipiter striatus*) and northern goshawks (*Accipiter gentilis*). We suspect a high proportion of birds arriving in the alpine were elevational migrants of local origin. Some forest birds, such as nuthatches and pine siskins (*Carduelis pinus*), certainly moved up the mountain to track emerging food resources (insects/ flower/ fruit) from snow melt and green-up. For North America, over 200 species of birds were recorded using alpine and sub-alpine habitats in late summer (literature and field surveys, URL: http://www.forestry.ubc.ca/alpine/index.htm ).

There are a number of reasons why alpine habitats are suitable for fall migrants (Table 4). In late summer, food resources have declined at lower elevations whereas in the alpine, late July to early September is the peak period of flowering and invertebrate emergence (Körner 1999). Migrants from the north use alpine and sub-alpine habitats as refueling points. The proximity of alpine habitats to forest, grasslands, shrub steppe or coastal habitats at lower elevations means that animals can move between these habitats in a short time. In late summer, few robins are observed on low elevation coastal breeding areas, a time when large numbers are observed in nearby alpine and sub-alpine habitats, as well as in lowland berry-rich wetlands (J.N.M. Smith, pers. comm.). Rufous hummingbirds move up to sub-alpine meadows and parklands in late summer and defend territories around flower patches (Sutherland et al. 1982). Territorial boundaries of migrant hummingbirds shift daily in relation to temporal patterns of flowering plants such as paint brush (*Castilleja sp*.) or columbine (*Aquilegia* sp, Gass and Lertzman 1980, Gass and Sutherland 1985). From mid August to early September, alpine grasslands support large numbers of grasshoppers that are eaten by kestrels (*Falco sparverius*), mountain bluebirds and Townsend's solitaire (S.Ogle, pers. obs.). Yellow-rumped warblers (*Dendroica coronata*), a common passerine migrant

in the alpine, fly-catch from cliff edges in late September. The increasing abundance of prey attracts predators. Migrating raptors use the open mountain terrain to hunt for landbirds and small mammals, often using updrafts along cliff faces and ridges. The duration that individual altitudinal migrants spend in the alpine is unknown, but temporal patterns are most likely related to resource availability and may vary with species. Some altitudinal migrants could move to alpine and sub-alpine areas on a daily basis and spend their nights at lower elevations. Band-tailed pigeon (*Columba fasciata*) could be one such species where availability of late summer fruits in the sub-alpine such as huckleberry, crowberry (*Empetrum nigrum*), and bearberry, may help compensate for the loss of traditional fruit and nutbearing shrubs due to habitat loss at lower elevations.

In summary, about one third of the vertebrate fauna in Washington and Oregon use high elevation habitats at some period in their life history. The chief period of occupation for many species is between late July and late October (Figure 4). Thus, the biodiversity of high elevation ecosystems is often greatly underestimated, and, clearly, we need to consider life history periods outside the breeding season.

**Winter residents.** Few wildlife species winter in alpine areas, and fewer still remain active in winter. Some birds, including white-tailed ptarmigan, raven (*Corvus corax*), and rosy finch remain at the highest elevations during winter, and a few arctic or northern species like snowy owls (*Nyctea scandiaca*) and snow buntings (*Plectrophenax nivalis*) migrate south to use alpine areas in the Pacific Northwest. Rosy finches forage for exposed seeds on windswept alpine ridges (French 1959). Gray jays (*Perisoreus canadensis*), raven, Clark's nutcracker, and hardy songbirds like golden-crowned kinglets (*Regulus satrapa*) and dark-eyed juncos (*Junco hyemalis*) use tree islands in sub-alpine parklands in winter. A number of mammals make use of alpine and sub-alpine habitats in winter, including pika, white-tailed jackrabbits, mountain caribou, and mountain goats and their predators, foxes, coyotes, pine marten (*Martes americana*), wolverine, Lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), and mountain lion hunt along or above the treeline. Mammals develop thick insulated fur coats and are adept at finding shelter from alpine winds and winter temperatures. Three *Myotis* bats hibernate in sub-alpine winter caves or mines in Washington and Oregon. Most species use snow roosts or snow burrows for sleeping or during storms. White-tailed jackrabbits winter as individuals at the interface of wind swept ridges and the krummholz (Braun and Streeter 1968). For

marmots and ground squirrels that hibernate overwinter at high elevations, choice of burrow and amount of snow cover can be crucial to overwinter survival (Armitage 1999, Arnold 1990b, 1993). Pika, weasels and voles remain active in the sub-nivean layer where they have temporary reprieve from life theatening predators and winter storms.

## 6. Threats/Status for Wildlife Species

Most local and regional scale threats to wildlife species in alpine and sub-alpine habitats relate to human activities (Table 5). These include on- and off-site impacts due to ski resorts, hiking, mountain biking, climbing, fishing, group camping, off-road use of all-terrain vehicles, and helicopter-supported skiing, hiking, fishing and sight-seeing activities. In Mt. Rainier National Park, 12% of plants (107 of 894 species) and 14% of birds (21 of 147) are exotic species (Filley 1996). Other potential threats to ecological conditions in alpine areas include livestock grazing, mining, montane forestry, ground source contaminants, and barriers imposed by roads and trails (Braun et al. 1976, Larison et al. 2000). Except in a few parks, anthropogenically-induced impacts on alpine wildlife are not well monitored in Washington and Oregon.

### Local Impacts

**Wildlife conflicts in winter—downhill skiing and other alpine recreation activities.** Winter may be a period of great sensitivity, with human disturbances possibly causing the most adverse impacts on wildlife species. At this time, many grouse and ungulates occur in social groups or flocks and live at about the same elevational range as downhill ski facilities. On Vancouver Island, British Columbia, for example, white-tailed ptarmigan move from an average summer elevation of 1676 m (5,500 ft) down to treeline (1372 m, 4,500 ft) in winter (K. Martin, unpubl. data), while blue grouse move up to treeline

### Table 5. Land uses and possible threats in alpine and sub-alpine habitats

1. Ski area developments, on-site and off-site impacts
2. Hiking, fishing and hunting, especially with helicopter access
3. Mountain biking, rock climbing, para-gliding
4. Livestock grazing, especially sheep grazing
5. Mining, montane forestry
6. Airborne toxins, ground source contaminants

(King 1971, Smith et al. 1997). Winter ptarmigan flocks can include individuals from a distance of 23 km (14 mi, Hoffman and Braun 1975). Thus activities that impact flocks adversely may be observed over considerable distances.

Ski resort developments impose both on- and off-site impacts. Tourist activities in winter cause serious disturbance to black grouse (*Tetrao tetrix*), now found mainly in mountain forests due to extensive habitat loss at low elevations in central Europe (Storch 2000). The construction of ski stations in the Alps between 1950 and 1980 removed or reduced the quality of many black grouse winter habitats in France and Germany. Ski stations also cause major disturbances in winter feeding behavior, winter range and disturbance on leks resulting in dramatic population declines (Menoni and Magnani 1998, Zeitler and Glanzer 1998). Downhill and back country skiers searching for deep powder snow cause additional disturbance as these sites are also sought by grouse for snow burrows to escape the cold and predators (A. Zeitler, pers. comm.). The use of explosives to precipitate controlled avalanches cause ptarmigan to flush from snow burrows on ski areas in the Alps and Pyrenees (Menoni and Magnani 1998). Mountain goats are particularly sensitive to disturbance as they do not habituate to alpine recreational activities such as helicopter hiking or skiing (Côté 1996).

Adverse effects from ski hill facilities can occur year-round. After a road and chairlifts were constructed in 1960-1961 at Cairngorm Mountain in the Scottish highlands, allowing easier human access, numbers of crows and gulls on the mountain increased, largely sustained by food scraps (Watson 1979, 1991), but they also preyed on ptarmigan (*L. mutus*) eggs and dotterel (*Charadrius morinellus,* Nethersole-Thompson and Watson 1981, Thompson and Whitfield 1993). Density and breeding success of red grouse (*L. l. scoticus*) and ptarmigan on Cairngorm Mountain did not change in relation to skier activities, but ski lift cables caused significant mortality for both species when birds flew into them, and harassment by free-running dogs was reported (Watson 1982). In France, 91 dangerous ski cables were identified and measures proposed to improve visibility of these cables (Observatoire des Galliformes de Montagne 1997). Mortality of grouse due to ski area activities is almost certainly additive since it occurs in late winter and early spring, after the period when highest overwinter mortality in grouse populations was recorded in Norway (Frilund 2000) and in Iceland (O.K. Nielsen, pers. comm.).

**Wildlife conflicts in summer.** Alpine species may be heavily impacted directly by recreational pressures

during the breeding season. Recreational activities like rock climbing or hang gliding can disturb cliff-nesting raptors or ungulates with young. No differences were observed in reproductive success of black grouse inside and outside areas visited by tourists in the French Alps (Miquet 1986). However, black grouse use of habitat close to a heavily frequented path in a French National Park was reduced by 40 to 50%, perhaps due to the presence of wandering dogs (Houard and Mure 1997). Alpine marmots in the Swiss and French Alps adjust well to human presence once they become habituated to large numbers of hikers (Louis and Le Berre 1997, Neuhaus and Mainini 1998). However, chamois (*Rupicapra rupicapra*) and mouflon (*Ovis orientalis*) that are hunted in the Alps and Pyrenees retreat to more inaccessible alpine areas when they encounter humans, even when there are high numbers of hikers. Mouflon came down to forage on alpine grasslands when there were few hikers or when fog reduced visibility, but they quickly retreated upslope when disturbed (J.-L. Martin and K. Martin, pers. obs.). Thus, alpine ungulates are less likely to habituate to disturbance from tourists where they are hunted than where they are protected, and the impact of disturbance will be greatest when high alpine refuges offer only low quality forage.

Visitors feeding wildlife in parks and recreation areas can cause local negative impacts. Wildlife feeding can change habitat use patterns and inappropriate food can be injurious to health of the animals. Wildlife feeding may result in naivete, particularly of young animals. Mountain goats and bighorn sheep have been killed by cars on mountain roads because they were unwary and associated cars with food (K. Martin, pers. obs.), or because they were attracted to road salt (M. Festa-Bianchet, pers. comm.). Densities of such generalist predators as chipmunks, corvids or canids, or herbivore species such as marmots or golden-mantled ground squirrels may increase due to accidental or intentional feeding of wildlife. This might change predation risk regimes for alpine species due to a direct increase in predator abundance or the amount of time predators spend in the alpine (Watson 1982).

Grazing by domestic species in alpine sites, particularly by sheep, reduces habitat cover for predator avoidance and may reduce forage quality for native herbivores (Braun 1980). If areas are heavily grazed and trampled, species composition can change dramatically, with many herbaceous plants being extirpated locally. Large areas of the Okanogan Highlands in the Paysaten Wilderness have been heavily grazed by thousands of domestic sheep since the late 1800s. Recently, the U.S. Forest Service reduced the number of sheep on this area to a few

hundred. Studies on long-term effects of sheep grazing in alpine and sub-alpine grasslands are needed for this region. However, other studies have suggested that domestic livestock have a greater impact on native ungulates through transmission of exotic diseases rather than by grazing competition (Onderka et al. 1988, Foreyt et al. 1994, Pybus et al. 1996).

## Regional Impacts

**Air and water quality.** Alpine areas are considered pristine habitats where the air is pure and water is clean and both are continually renewed by wind and snow melt. However, emerging information suggests that alpine sites are not as pristine as we think. Mt. Rainier National Park in western Washington consistently had the highest average weekly concentrations of ozone (Brace and Peterson 1999). Although, a natural component of the earth's troposphere, in high concentrations ozone can injure vascular plants and be potentially hazardous to human health (Lippman 1989). Ozone concentrations are higher at high elevations, which is partly a natural atmospheric phenomenon, but also partly due to upwind transport of pollutants from lower elevation urban areas. Thus, alpine plants and animals in Washington are exposed to high ozone concentrations on warm and sunny days (Brace and Peterson 1999). Blais et al. (1998) found high levels of organochlorines in mountain parks in western Canada. Airborne toxins may influence snow melt patterns in alpine sites and, thus change environmental conditions for wildlife species as well as quality of the water supply for nearby urban sites.

Alpine habitats are similar to arctic ecosystems because both have shallow soils that are impervious much of the year and have low levels of biological activity (e.g., soil bacteria, Chapin and Körner 1994, Körner 1999); thus neither are effective at filtering toxic materials. They differ in that the alpine atmosphere is less resistant to airborne transport of particulate matter. Air and water quality in many mountain wilderness sites in western North America are also relatively more compromised than arctic systems given their proximity to large urban centres such as Seattle, Vancouver, and Denver (Brace and Peterson 1998).

Ground source contaminants are also a potential risk to wildlife at high elevations (Table 5). In the metal rich ore belt of the Colorado Rocky Mountains, high concentrations of cadmium, an extremely toxic but naturally occurring heavy metal, were found in white-tailed ptarmigan tissue and also in their foods (Larison et al. 2000). High cadmium concentrations were associated with kidney damage, particularly for overwintering female ptarmigan. This study also

reported a possible reduction in ptarmigan survival and lower population densities in the ore belt regions. Since willow was shown to biomagnify cadmium, other herbivores such as elk and deer living in these alpine regions could also be at risk of cadmium toxicity (Larison et al. 2000). Effects of changes in the quality of air, water and soils on alpine wildlife merit further study.

**The increasing value of high elevation habitats**. Alpine and sub-alpine areas have increased in value as wildlife habitat, given changes in habitats or processes at low elevations. Wildlife species that formerly used habitats over a broad range of elevations are becoming restricted to the upper elevations of their former range. The problem of upward shifting is well advanced in central Europe. Here most forest grouse species that originally occupied a range of habitats from low elevation bogs, heaths, and moorlands up to the sub-alpine treeline have been extirpated from the low elevations in the past century, due to intensive agricultural and forestry activities. Black grouse in central Europe are now 'de facto' sub-alpine parkland species due to the current unsuitability of traditional low elevation habitats (Storch 2000). The relative productivity for wildlife species in high and low elevation habitats was not established previous to extirpation at low elevation. However, high elevation habitats regularly experience total reproductive failure and many species are endangered (Storch 2000). Formerly, high elevation populations may have been rescued in years of low production by low elevation populations, but this option is less and less possible. Predation risk might be increasing at high elevations if predators have increased food availability as a result of human presence. In Europe, wolves and brown bears are largely restricted to high latitudes and mountain habitats (Sutherland and Reynolds 1998). For large carnivores, the retreat to high elevation habitat patches results in species distributions being more fragmented than formerly (Breitenmoser 1998). Eurasian lynx (*Lynx lynx*) in Switzerland may travel over 100 km to an adjacent mountain group to circumvent barriers imposed by highways and densely settled areas (Breitenmoser 1998).

On first consideration, it might appear that we need not worry about mean elevational increases for species in the Pacific Northwest. However, in western Washington and Oregon, low elevation coniferous forests have been converted to intensive agricultural, industrial or high density urban areas and, many low elevation wetlands have disappeared (Edge 2001, Ferguson et al. 2001). Hence, wildlife species that traditionally occupied a broad elevational range of habitats here have also experienced significant range reduction, accompanied with an 'upward shift', including such species as white-tailed jackrabbit, western toad, other amphibians, blue grouse, ruffed grouse, wolf, and other large predators. For example, blue grouse numbers have declined in many low elevation areas of Washington and Oregon, while high elevation populations remain unchanged (M.A. Schroeder, Washington Department of Fish and Wildlife, pers. comm.). In the case of grizzly bear, the 'upward shift' in population distribution is also facilitated by greater conflicts with humans at low elevations, in addition to low elevation habitat loss.

For wildlife species living at higher elevations, we need to determine which species have experienced the largest elevational shifts and whether any appear in difficulty. One problem relates to potential increased energetic costs of living at higher elevations as discussed in Section 5, as well as the impact on population viability of more frequent and greater stochasticity in annual production (Widmer 1993). We should establish whether wildlife populations at low elevation rescue high elevation populations following years of reproductive failure at high elevations. Risks to wildlife population viability in spatially separated high elevation 'islands' that result from removal of low elevation populations will increase due to habitat fragmentation and reduced effective population size.

## Ultimate factors—climate change and global warming

Climate change has strong impacts on wildlife species at high elevations (Burton 1995, Jenik 1997, Inouye et al. 2000). Increased concentrations of $CO_2$ available for photosynthesis and changes in temperature and moisture availability increase growth rates, abundance and elevational range of many alpine plants at higher elevations (Körner 1999). In Austria, surveys of alpine plants growing 15-20 m from the peak in 1992 and 1993 found 26 (87%) of 30 mountains had higher species richness than surveys done in identical sites 40 to 100 years earlier (Grabherr and Pauli 1994, Price and Barry 1997). Upslope movement rates for alpine plants for these mountains were calculated as 1 to 4 m (3.2-13 ft) over a 10 year period (Grabherr and Pauli 1994). In the context of global warming, the small-scale patterns of environmental conditions in the alpine zone, allow 'space for time' studies, because vegetation has had no time to adjust to these temperature gradients and, thus is likely to produce a more realistic picture of longterm responses to changing climates (Körner 1999).

*Fig. 5. Cattle Creek in Stein Park shows range of habitat types from riparian valley to mountaintop with treeline going up much higher on north side (left) than on the drier south side. Photo by Steve Ogle, August 1998.*

Research on wildlife responses to climate change is beginning to emerge (Inouye et al. 2000). With climate change, upper limits of plant growth will increase, and food availability per unit area for alpine herbivores may increase. However, with the increasing altitude of treeline, another expected consequence of climate change, alpine habitats will become more fragmented with smaller and more isolated patches. Animals living in these patches will have smaller populations and be required to disperse longer distances to other alpine patches, or pay the consequences of not dispersing (Martin et al. 2000, Roland et al. 2000).

Alpine animals are well adapted for living in cold climates, but most have not developed sophisticated mechanisms for coping with warm temperatures (Smith 1974). Daytime ground temperatures in the Colorado alpine regularly exceeded 45°C, and thus cooling can be a concern for alpine birds in summer (Wiebe and Martin 1997). Alpine animals cool themselves by going underground or by moving to snowfields. In the low elevation alpine of Washington and Oregon, an increase of 1 to 2°C in mean temperature could have a large impact on the extent of snow pack and snowmelt patterns. Faster melting snow fields might not persist through summer (Figure 5). Fewer or smaller snowfields leave animals with restricted habitat availability and longer dispersal distances to other habitats. With less area to search, predators may be more successful in capturing prey.

In response to increasing temperatures in spring, pied flycatchers (*Ficedula hypoleuca*) increased their egg size over a 19-year period in the mountains of northern Finland; larger eggs had higher hatching success, but there was no improvement in numbers of young raised (Järvinen 1994, 1995). Increasing spring temperatures over a 28-year period were also correlated with earlier initiation of egg laying and larger clutches (Järvinen 1994). However, duration of abundant food resources in late summer will decrease if plant phenology gradients are reduced by faster snow melt. Global warming is thus expected to have large consequences for high elevation wildlife species, including reduced habitat availability and suitability, reduced duration of food abundance, but perhaps greater per unit area of food availability and possibly increased predation risk. Unfortunately, empirical data for alpine plants and climate change have been ambiguous with responses by plant species being quite specific (Körner 1999). Overall responses will be difficult to predict until the key ecological or physical factors are determined. For example, temperature may be less important than moisture in determining the distribution of mountain flora and fauna (Woodward 1992). Long-term monitoring programs for alpine and sub-alpine wildlife will have high efficacy, as even small increments in warming have significant impacts on habitat quantity and quality for breeding and migration.

## 7. Information Needs and Conservation Recommendations

**Need to develop concerns for alpine conservation and management.** Probably the largest concern about alpine habitats is *the lack of concern* about high elevation conservation. The idea prevails that much alpine area is already protected, maybe too much, and that most alpine areas are inaccessible and thus not at great risk. Alpine areas are given lower priority than low elevation habitats because they have modest diversity of breeding species. Such attitudes account for a lack of concern and knowledge regarding status and trends of alpine wildlife populations, in particular

for non-game species. Most research for alpine fauna has been done in summer and, thus our knowledge of seasonal use of alpine areas is limited. We are not in a good position to detect early population declines, especially if ecological processes such as predation are shifting at large cross-habitat scales.

Wildlife research is needed to determine the important ecological processes and habitat functions required by both 'alpine obligate' and 'alpine tolerant' vertebrate species. Research is also needed to improve predictions on how wildlife species will cope with changing climatic and environmental conditions. Life history studies are needed for high elevation populations of 'alpine tolerant' species that are experiencing extensive habitat loss at low elevations. Better understanding is required about the importance of maintaining connectivity across time and space for species with seasonal altitudinal shifts. For ungulates and large carnivores, we need to ensure that alpine species have access to valley lowlands and other important wintering habitats. In national parks and wilderness sites, more research and application is required on restoration of impacted alpine grasslands and sub-alpine meadows, particularly in the North Cascades Range (Rochefort and Gibbons 1992). Finally, to detect and predict the ecological effects of global climate change, it will be crucial to establish long-term alpine habitat and wildlife monitoring programs similar to programs in the Austrian Alps (Grabherr and Pauli 1994), northern Finland (Järvinen 1994, 1995), or in the Rocky Mountains (Inouye et al. 2000).

**Migration corridors in the alpine: the need to consider habitat connectivity.** Alpine habitats function as seasonal migration and dispersal corridors for wildlife. High latitude birds use alpine and sub-alpine habitats as migration highways to move from northern breeding territories to southern winter areas (Box 4). Nocturnal and diurnal migrants may use mountain ridges for navigation (Bruderer 1982). The continued loss of low elevation migration habitat such as riparian and coastal areas strengthens the need to understand and manage for such ecological functions as alpine migration corridors. Increasing use of alpine areas is expected by large area-sensitive animals, particularly predators, where landscapes have been fragmented.

The issue of connectivity between high and low elevation habitats is an important biological and management question. Parks in the Rocky Mountains have a disproportionate amount of their habitat at high elevation, and most parks do not contain year-round habitat requirements for a number of wildlife species (Weaver et al. 1996). For example, some elk are year-round residents in Banff National Park, but others are migratory; some migratory elk use up to six different management jurisdictions in a single year, including both hunted and non-hunting zones in two provinces (Woods 1991). For alpine residents, we need to ensure that connectivity is maintained from alpine habitats to adjacent lower elevation forests and valley bottoms (Figure 5). In mountain habitats, landscape context can be critical as access to large areas may contain bottlenecks (Noss et al. 1996). Urban areas and roads in valley bottoms can sub-divide populations or restrict access to seasonally-used habitats. Mountain passes are also likely important for seasonal access or population connectivity, and these tend to be where roads, trails and recreational huts are situated.

The most severe wildlife-human conflicts occur in mountain landscapes with narrow valleys that are densely settled or developed. Unfortunately, mammalian wildlife in western North America often require access to valley bottoms to move between mountain chains, since alpine areas tend to be closed off by cliffs. Thus the presence of urban or highway development is almost guaranteed to interrupt wildlife movements, act as a dispersal barrier and fragment populations of large ungulates and predators. All U.S. Interstate highways in mountains impede movements of large mammals (C.E. Braun, pers. comm.). Also, this is a particularly important problem in large mountain parks such as Banff National Park where urban developments and major highways in the narrow Bow Valley have greatly impeded movements of large mammals and fragmented their populations (Noss et al. 1996). Species vary in their willingness to cross such dispersal barriers and their wariness when doing so (Weaver et al. 1996). Determining the ecological value of the alpine as migration habitat and minimizing interruptions of wildlife movements in mountains are two research priorities.

**Changes in ecological parameters at high elevations.** Increases in predator density or the amount of time predators spend in the alpine could significantly increase the predation risk for alpine and sub-alpine species, as well as for 'upward shifted' alpine tolerant species. Medium- and large-sized predators such as grizzly, wolf or lynx that do not persist easily in high density urban areas have probably moved higher. For them, ungulates provide a reliable food resource through the winter period. Forestry activities at high elevation may also result in changes to wildlife communities. Research is needed on the influence of montane forest cutting in the Pacific Northwest on distribution and abundance of generalist predators, and consequent impacts on

survival and reproduction of wildlife in adjacent alpine and sub-alpine habitats.

Increases in recreational use of high elevation areas increases food availability for generalist predators. High elevation habitats are generally unsuitable for crows or Steller's jays, but populations can exist if there are dwellings or dumps nearby (Smith et al. 1997). Along the Cascade Crest, crows occur in ski areas and towns. Raven densities may increase along roads as a result of road kills. A study during the breeding season in northern Finland found more magpies and crows around three ski hill centres than in pristine forest of the same type and age in the region. Also, predation of artificial nests was much higher for the ski hill centres than the undisturbed forest (J. Jokimaki, unpubl. data, jukka.jokimaki @urova.fi)

Human activities at lower elevations might also influence ecological processes in the alpine. Mid-sized predators like ravens and coyotes have substantial home ranges and, could easily travel 5 to 10 kilometers from lower elevations to the alpine, but it is unknown whether they do so. Over-winter survival of generalist predators is improved by road-kills, dumps in adjacent urban areas, or from feeding in backyards at holiday homes or ranchettes in montane forest. Generalist predators no longer depend year-round on traditional prey to survive when anthropogenic food supplies are available, but if they kill the natural prey they encounter even in just one season, they could profoundly impact alpine prey population densities. Given that many high elevation wildlife species are long-lived, a reduction in adult survival has a relatively higher demographic impact than for r-selected species. We need to conduct field research on possible disturbance factors that increase generalist predator densities in or near high elevation areas, whether these predators spend more time at high elevation, and whether these increases significantly impact alpine wildlife populations. At the same time, we need to manage garbage and educate people to avoid feeding wildlife in and adjacent to alpine areas to ensure natural population densities of generalist predators.

**Coexistence of alpine wildlife communities and winter recreation activities.** Ski areas and adjacent resorts have negative ecological impacts on alpine habitats such as soil erosion from sub-alpine forest cutting, which can in turn impact water quality. Wildlife may be displaced or their movements restricted due to cleared areas for ski runs or building facilities. Snow making for fall skiing occurs in many North American ski operations, and can draw down water tables in the drier interior mountain conditions (Legault 1997). Little is known about impacts on alpine plants and animals of additives (ice-nucleating bacteria, fertilizer) to water to improve snow making efficiency (Legault 1997). Before approval of skiing and other recreational developments in alpine and montane habitats, careful surveys should be done in winter to determine which areas to avoid to minimize wildlife conflicts. Patterns of winter habitat use by high elevation wildlife species (e.g., blue grouse, ptarmigan, elk, bighorn sheep) should be determined before facilities are approved. For example, after it was determined that a proposed expansion of ski runs and lifts disrupted an elk migration route in Colorado, the Aspen Skiing Company revised their plans in consultation with the Pitkin County Commission, Aspen town council, Colorado Division of Wildlife, and Sierra Club local chapter (Giezentanner 1994, URL: http://www.skiaspen.com/environment). Construction of ski runs and buildings was done in winter. Trees were cut, but no bulldozer grading was done to avoid disturbing sub-alpine vegetation. Little is known, or being investigated, regarding potential impacts to alpine or sub-alpine species from other disturbances associated with ski facilities, such as large volumes of sewage and garbage, compacted sub-alpine vegetation, light pollution from night skiing and, the consequences of later spring green-up caused by delayed snow melt from compacted snow and snow making (Legault 1997).

In the past two decades, there has been a dramatic increase in alpine cross country ski touring and, in the use of helicopters to access remote areas for skiing, fishing, and hiking. Such activities do not result in many visits per mountain, however, the overall size of area impacted has increased dramatically. The impact of such disturbances on wildlife are difficult to monitor, control or to predict. Ski touring groups in Bavaria cause considerable disturbance to wintering populations of grouse and ungulates (Zeitler and Glanzer 1998). Proactive multi-partner consultations have had good success in designing ski touring routes with leave areas for wintering wildlife in Bavaria (Suchant and Roth 1998, Zeitler and Glanzer 1998).

The increased use of alpine facilities in fall, particularly with late summer hiking and mountain biking, may result in conflicts with seasonal movements of wildlife from late summer habitats to winter sites. Careful evaluation of habitat use should be done and seasonal wildlife travel corridors determined in advance of designing and approving new ski developments or expanding existing operations. The effects of ski developments cover a much larger area than proposed development sites, particularly since they are often positioned at the headwaters of watersheds (Legault 1997). A secondary effect of ski area developments is the

urbanization of mountain valleys. Increasingly, ski resort areas are becoming amenities to support luxury second home communities. Reviews of proposed new developments or expansions of ski resort areas should consider off-site impacts from this secondary urbanization, including all concerns relevant to urban areas near alpine habitats. Potential impacts should be evaluated at a sufficiently large scale to include connectivity issues discussed earlier for maintaining viable mountain wildlife populations. Proposed alpine recreational developments should demonstrate that they have allowed for maintenance of normal ecological processes.

## 8. Summary

The alpine zone consists of rugged, partially vegetated terrain with snowfields and rocky ridges, above the natural treeline. Alpine ecosystems are structurally simple with few plant species compared to most lower elevation habitats. In Washington and Oregon, the main wildlife habitats are (1) alpine grasslands and shrublands, and (2) sub-alpine parklands. These habitats are characterized by high winds, prolonged snow cover, steep terrain, extremes of heat and cold, and intense ultraviolet radiation. With increasing elevation, time for breeding decreases and environmental stochasticity increases; at the highest elevations, hypoxic conditions add additional energetic living costs. Other ecological costs may also be high, such as high predation risk in the open alpine habitats, and the need for seasonal movements from patchy breeding habitats to wintering areas. These factors result in short, intense breeding seasons for wildlife.

About one third of the vertebrate fauna (188 species) in Washington and Oregon use alpine or sub-alpine habitats at some period in their life history. These include 65 species of mammals, 112 birds and 11 reptiles and amphibians. Only a few species such as white-tailed ptarmigan, hoary marmots and mountain goats live exclusively in the alpine, while the majority breed in both alpine and lower elevation habitats or use high elevation habitats during migration. For true alpine breeders, some life history traits may vary with altitude as reproductive rates are often lower and development times longer, with accompanying increases in longevity. For wildlife species breeding across elevational gradients, reproductive success at high elevation appears similar to those for populations at lower elevations. However, with compressed reproductive seasons, wildlife at high elevation produce fewer offspring in a season.

An unexamined aspect of biodiversity for high elevation ecosystems is their use by migrating wildlife during late summer and fall. From late July through October, alpine areas support a rich diversity and abundance of birds and mammals that move up from lower elevations, as well as high latitude avian migrants. This is a time when alpine habitats offer rich food resources, and productivity in many low elevation habitats has declined. Thus, we need to include life history periods outside the breeding season when evaluating high elevation habitats for wildlife. Connectivity is a key ecological process for high elevation wildlife populations. Connectivity needs to be maintained (1) among patchy alpine habitats, (2) along mountain corridors for north-south migrants, and perhaps most importantly (3) between alpine and adjacent lower elevation habitats and valley bottoms for elevational migrants.

Despite being highly valued for their intrinsic beauty and wildness, alpine vertebrates and high elevation habitats are a neglected area for research and management. Even though currently most alpine species appear secure in mostly stable habitat conditions, change within and adjacent to alpine and sub-alpine habitats is happening rapidly and over extensive areas. Alpine ecosystems have experienced large increases in amount and kinds of human use, with some areas showing significant deterioration caused by recreational activities, livestock grazing, mining, and airborne contaminants. High elevation habitats are vulnerable to erosion, especially near melting snowfields or when soil crusts are broken above volcanic ash, and vegetation recovers slowly after such disturbances. To prevent elevated predation risk for alpine wildlife, we should avoid inadvertent increases in food supplies for generalist predators in and near high elevation habitats. On a landscape scale, developed valley bottoms constitute dispersal barriers for many wildlife species with seasonal vertical movements. Since we lack comprehensive understanding of what is required to maintain ecological processes in alpine habitats and have limited experience in restoring these sensitive ecosystems, the precautionary principle is strongly advised for managing alpine and sub-alpine communities. Finally, we need to establish long-term monitoring programs to detect and predict the ecological effects of climate change on alpine habitats and wildlife populations.

## 9. Acknowledgments

## 10. Literature Cited

Agee, J.K. and L. Smith. 1984. Subalpine tree establishment after fire in the Olympic Mountains, Washington. Ecology 65: 810-819.

Allee, W. C. and K. P. Schmidt. 1951. Ecological Animal Geography. John Wiley and Sons, Inc. New York.

Armitage, K. B. 1986. Individuality, social behavior, and reproductive success in yellow-bellied marmots. Ecology 67: 1186-1193.

———. 1999. Evolution of sociality in marmots. Journal of Mammalogy 80: 1-10.

Arno, S. F. and R.P. Hammerly. 1984. Timberline: Mountains and arctic forest frontiers. The Mountaineers, Seattle, U.S.A.

Arnold, W. 1990*a*. The evolution of marmot sociality: I. Why disperse late? Behavioural Ecology and Sociobiology 27: 229-237.

———. 1990*b*. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. Behavioural Ecology and Sociobiology 27: 239-246.

———. 1993. Social evolution in marmots and the adaptive value of joint hibernation. Verh. Deutsch Zool. Ges. 86: 79-93.

Bätzing, W. 1991. Die alpen: entstehung und Gefährdung einer europäischen kulturlandschaft. Beck, Munich, Germany.

Beason, R.C. 1995. Horned lark *(Eremophila alpestris).* Pages 1-24 *in* A. Poole and F. Gill, editors. The birds of North America, No. 195. The Academy of Natural Sciences; Philadelphia, USA.

Billings, W. D. 1989. Alpine vegetation. Pages 392-420 *in* W. D. Billings and R. K. Peet, editors. Terrestrial vegetation of North America. Paragon Books.

———, and H. A. Mooney. 1968. The ecology of arctic and alpine plants. Biological Review 43: 481-529.

Blais, J. M., D, W. Schindler, D. C. G. Muir, L. E. Kimpes, D. B. Donald, B. Rosenburg. 1998. Accumulation of persistent organochlorine compounds in mountains of western Canada. Nature 395: 585-588.

Böhn, C., and A. Landmann. 1995. Nest-site selection and nest construction in the Water pipit *(Anthus spinoletta).* Journal für Ornithologie 136: 1-16.

Brace, S. and D. L. Peterson. 1998. Spatial patterns of tropospheric ozone in the Mount Rainier region of the Cascade Mountains, U.S.A. Atmospheric Environment, 32: 3629-3637.

Braun, C. 1969. Population dynamics, habitat, and movements of White-tailed Ptarmigan in Colorado. Ph.D. thesis, Colorado State University, Fort Collins, Colorado.

Braun, C. E. 1971. Habitat requirements of Colorado white-tailed ptarmigan. Proceedings of Western Association of State Game and Fish Commissioners 51: 284-292.

Braun, C. E., and R. G. Streeter. 1968. Observations on the occurrence of white-tailed jackrabbits in the alpine zone. Journal of Mammalogy 49: 160-161.

Braun, C. E., R. W. Hoffman, and G. E. Rogers. 1976. Wintering areas and winter ecology of White-tailed Ptarmigan in Colorado. Special Report No. 38, Colorado Division of Wildlife, Denver, Colorado, 38pp.

Braun, C. E., R. K. Schmidt, and G. E. Rogers. 1973. Census of Colorado white-tailed ptarmigan with tape-recorded calls. Journal of Wildlife Management 37:90-93.

———. 1980. Alpine bird communities of western North America: implications for management and research. Pages 280-291 *in* R. M. DeGraff and N. G. Tilghman, compilers. Workshop Proceedings: Management of western forests and grasslands for nongame birds. U.S. Department Agriculture Forest Service General Technical Report INT-86.

———, K. Martin, and L. A. Robb. 1993. White-tailed ptarmigan *(Lagopus leucurus).* Pages 1-24 *in* A. Poole, and F. Gill, editors. The birds of North America, No. 68. Philadelphia: The Academy of Natural Sciences; Washington, D. C., USA.

Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors. Biological Conservation 83: 279-289.

Bronson, M. T. 1979. Altitudinal variation in the life history of the golden-mantled ground squirrel *(Spermophilus lateralis).* Ecology 60: 272-279.

Bruderer, B. 1982. Do migrating birds fly along straight lines? Pages 3-14 *in* F. Papi and H. G. Wallraff, editors. Avian Migration. Springer, Heidelberg.

Bullard, R.W. 1972. Vertebrates at altitudes. Pages 209-226 *in* M. K. Yousef, S. M. Horvath, and R. W. Bullard editors. Physiological adaptations, desert and mountain. Academic Press, New York, USA.

Burton, J. F. 1995. Birds and climate change. Helm, London, UK.

Campbell, R. W., N. K. Dawe, I. McTaggart-Cowan, J. M. Cooper, G. W. Kaiser, M. C. E. McNall, G. E. J. Smith. 1990 and 1996. The Birds of British Columbia. Volumes 1-3. University of British Columbia Press, Vancouver, Canada.

Cannings, R. A., R. J. Cannings, and S. G. Cannings. 1987. The birds of the Okanagan Valley. Royal BC Museum, Vicoria, BC, Canada.

Cannings, R. J., and S. G. Cannings. 1996. British Columbia, A Natural History. Douglas and McIntyre, Vancouver, Canada.

Capula, M, L. Luiselli, and C. Anibaldi. 1992. Complementary study on the reproductive biology in female adder, *Vipera berus (L.)* from eastern Italian Alps. Vie Milieu 42: 327-336.

Carey, C. 1980. Adaptation of the avian egg to high altitude. American Zoologist, 20: 449-459.

———, and K. Martin. 1997. Physiological ecology of incubation of ptarmigan eggs at high and low altitudes. Wildlife Biology 3: 211-218.

Carpenter, F. L., and M. A. Hixon. 1988. A new function for torpor: fat conservation in a wild migrant hummingbird. The Condor 90: 373-378.

Cassidy, K. M., C. E. Grue, M. R. Smith, and K. M. Dvornich, editors. 1997. Washington State Gap Analysis - Final Report. Volumes 1-5. Washington Cooperative Fish and Wildlife Research Unit, University of Washington, Seattle, USA.

Chapin, F. S. III, and C. Körner, editors. 1994. Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Springer-Verlag, New York, USA.

Chappell, C.B., R.C. Crawford, J. Kagan, D.H. Johnson, M. O'Mealy, G.A. Green, H.L. Ferguson, and W.D. Edge. 2001. Wildlife Habitats: descriptions, status, trends, and system dynamics. *In* D.H. Johnson and T.A. O'Neil (Manag. Dirs.) Wildlife-Habitat Relationships in Oregon and Washington. Oregon State University Press.

Cody, M. L. 1985. Habitat selection in grassland and open country birds. Pages 191-226 *in* Habitat selection in birds. Academic Press. New York, USA.

Corkran, C.C. and C. R. Thoms. 1996. Amphibians of Oregon, Washington, and British Columbia. Lone Pine, Vancouver, British Columbia.

Côté, S. D. 1996. Mountain goat responses to helicopter disturbance. Wildlife Society Bulletin 24: 681-685.

Crisafulli, C. M., and C. P. Hawkins. 1998. Ecosystem recovery following a catastrophic disturbance: Lessons learned from Mount St. Helens. *in:* M. J. Mac, P. A. Opler, C. E. Puckett Haecker, and P. D. Doran, editors. Status and trends of the nations biological resources. Volumes 1-2. U.S. Department of Interior, U.S. Geological Survey, Reston, Va.

Csuti, B., A.J. Kimerling, T.A. O'Neil, M.M Shaughnessy, E.P. Gaines, and M.M P. Huso. 1997. Atlas of Oregon wildlife: Distribution, habitat and natural history. Oregon State University Press, Corvallis, Oregon.

Daubenmire, R. 1954. Alpine timberlines in the Americas and their interpretation. Butler University Botanical Studies 11: 119-136.

Dobson, F. S. and J.O. Murie. 1987. Interpretation of intraspecific life history patterns: evidence from Columbian ground squirrels. American Naturalist 129: 382-397.

———, R. M. Zammuto, and J.O. Murie. 1986. A comparison of methods for studying life history in Columbian ground squirrels. Journal of Mammalogy 667: 154-158.

Douglas, G.W. and L.C. Bliss. 1977. Alpine and high subalpine plant communities of the north Cascades Range, Washington and British Columbia. Ecological Monographs 47: 113-150.

Dragon, S., C. Carey, K. Martin, and R. Bauman. 1999. Effect of high altitude and *in vivo* adenosine/β-adrenergic receptor blockade on ATP and 2,3BPG concentrations in red blood cells of avian embryos. Journal of Experimental Biology 202:2787-2795.

Edge, W.D. 2001. Wildlife communities of agriculture, pastures, and mixed environs. *In* D.H. Johnson and T.A. O'Neil (Manag. Dirs.) Wildlife-Habitat Relationships in Oregon and Washington. Oregon State University Press.

Edwards, O. M. 1980. The alpine vegetation of Mount Rainier National Park: structure, development and constraints. Ph.D. dissertation, University of Washington, Seattle, WA. 280 pp.

Ferguson, H.L., K. Robinette, K. Stenberg. 2001. Wildlife communities of urban habitats. *In* D.H. Johnson and T.A. O'Neil (Manag. Dirs.) Wildlife-Habitat Relationships in Oregon and Washington. Oregon State University Press.

Ferron, J., and J. P. Ouellet. 1989. Temporal and intersexual variations in the use of space with regard to social organization in the woodchuck *Marmota monax*. Canadian Journal of Zoology 67: 1642-1649.

Festa-Bianchet, M., M. Urquhart, and K.G. Smith. 1994. Mountain goat recruitment: kid production and survival to breeding age. Canadian Journal of Zoology 72: 22-27.

Filley, B. 1996. The big fact book about Mount Rainier. Dunamis House Publishing, Issaquah, Washington. 435 p.

Foreyt, W. J., K. P. Snipes, and R. W. Kasten. 1994. Fatal pneumonia following innoculation of healthy bighorn sheep with *Pasturella* haemolytica from healthy domestic sheep. Journal of Wildlife Disease 30: 137-145.

Franklin, J. F., and C. T. Dyrness. 1973. Natural Vegetation of Oregon and Washington. Oregon State University Press, Corvallis, USA.

Franklin, J. F., W.H. Moir, M. A. Hemstrom, S. E. Greene, and B. G. Smith. 1988. The forest communities of Mount Rainier National Park. U.S.D.I. National Park Service Scientific Monograph Series 19, Washington, D.C. 194 pp.

Frase, B. A. and R. S. Hoffman. 1980. *Marmota flaviventris*. Mamalian Species 135: 1-8.

Frilund, G. E. 2000. The effect of hunting on survival in willow ptarmigan *Lagopus l. lagopus*. M.Sc. Thesis, Norwegian University of Science and Technology, Trondheim, Norway. 39pp.

French, N. R. 1959. Life history of the black rosy finch. Auk 76: 158-180.

Frenzen, P. M. and C. M. Crisafulli. 1990. Mount St. Helens ten years later: past lessons and future promise. Northwest Science 64: 263-267.

Gaillard, J. -M., M. Festa-Bianchet, and K. G. Smith. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Research in Evolution and Ecology 13: 58-63.

Gass, C. L., and K. P. Lertzman. 1980. Capricious mountain weather: a driving variable in hummingbird territorial dynamics. Canadian Journal of Zoology 58: 1964-1968.

———, and G. Sutherland. 1985. Specialization by territorial hummingbirds on experimentally enriched patches of flowers: energetic profitability and learning. Canadian Journal of Zoology 63: 2125-2133.

Giezentanner, K. 1994. Wildlife and biodiversity analysis for the Snowmass Ski Development expansion. U. S. Forest Service report. Colorado, USA.

Grabherr, G. and M.G. H. Pauli. 1994. Climate effects on mountain plants. Nature 369: 448.

Grossman, D.H., D. Faber-Langendoen, A.W. Weakley, M. Anderson, P. Bourgeron, R. Crawford, K. Goodin, S. Landaal, K. Metzler, K.D. Patterson, M. Pyne, M. Reid and L. Sneddon. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Vol. 1: The National Vegetation Classification Standard. The Nature Conservancy.

Hannon, S.J. and K. Martin. 1996. Mate fidelity and divorce in ptarmigan: polygyny on the tundra. Pages 192-210 *in* J.M. Black, editor. Partnerships in birds, the study of monogamy. Oxford University Press, Oxford.

Hoffman, R. W. and C. E. Braun. 1975. Migration of a wintering population of white-tailed ptarmigan in Colorado. Journal of Wildlife Management 39: 485-490.

Houard, T., and M. Mure. 1997. Les tetras-lyre des vallons de Salese et Mollieres. Parc National du Mercantour. Domaine vital et influence du tourisme. Revue d'Ecologie (La Terre et la Vie), Supplemente 4: 165-197.

Houston, D. B., and V. Stevens. 1988. Resource limitation in mountain goats: a test by experimental cropping. Canadian Journal of Zoology 66: 228-238.

Inouye, D. W., B. Barr, K. B. Armitage and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Science 97: 1630-1633.

Järvinen, A. 1994. Global warming and egg size of birds. Ecography 17: 108-110.

———. 1995. Effects of climate change on mountain bird populations. Pages 73-74. *in* Guisan, A. et al., editors. Potential Ecological impacts of climate change in the Alps and Fennoscandian Mountains. Conservatoire et Jardin botaniques de la Ville de Genève: Geneva, Switzerland.

Jenik, J. 1997. The diversity of mountain life. Pages 199-231 *in* Messerli, B. and J. D. Ives editors. Mountains of the world: a global priority. Parthenon Publishing Group, London, UK.

Johnson, R. E. 1965. Reproductive activities of rosy finches, with special reference to Montana. Auk, 82: 190-205.

———. 1983. Nesting biology of the rosy finches on the Aleutian Islands, Alaska. Condor 85: 447-452.

Kiilsgaard, C. W. 1999. Oregon vegetation: mapping and classification of landscale level cover types. Final report submitted to the U.S. Geological Survey, Biological Resources Division: GAP Analysis Program, Moscow, Idaho.

King, D. G. 1971. The ecology and population dynamics of blue grouse in the subalpine. Msc thesis, University of British Columbia, Vancouver, Canada.

Kingery, H. E. 1996. American Dipper *(Cinclus mexicanus)*. Pages 1-28 *in* A. Poole, and F. Gill, editors. The birds of North America, No. 229. The Academy of Natural Sciences; Philadelphia. Washington, D. C., USA

Kirk, R. 1999. Sunrise to paradise: the story of Mount Rainier National Park. University of Washington Press, Seattle, USA.

Kollinsky, C., and A. Landmann. 1996. Altitudinal distribution of male black redstarts: are there age-dependent patterns? Bird Study 43: 103-107.

Körner, C. 1994. Alpine plant diversity, a global survey and functional interpretation. Pages 45-64 *in* F. S. Chapin III, and C. Körner editors. Arctic and alpine biodiversity: patterns, causes and ecosystem consequences. Springer-Verlag, New York, USA.

———. 1999. Alpine Plant Life: functional plant ecology of high mountain ecosystems. Springer-Verlag, Heidelburg, Germany.

Krajick, K. 1998. Animals thrive in an avalanche's wake. Science 279: 1853.

Kuramoto, R. T. and L. C. Bliss. 1970. Ecology of subalpine meadows in the Olympic Mountains, Washington. Ecological Monographs 40:317-347.

Landmann, A. and N. Winding. 1993. Niche segregation in high-altitude Himalayan chats (Aves, Turdidae): does morphology match ecology? Oecologia 95: 506-519.

———, and ———. 1995*a*. Adaptive radiation and resource partitioning in Himalayan high-altitude finches. Zoology – Analysis of Complex Systems 99: 8-20.

———, and ———. 1995*b*. Guild organisation and morphology of high-altitude granivorous and insectivorous birds: convergent evolution in an extreme environment. Oikos 73: 237-250.

Lanner, R. M. 1988. Dependence of Great Basin Bristlecone pine on Clark's nutcracker for regeneration at high elevations. Arctic and Alpine Research 20: 358-362.

Larison, J. R., G. E. Likens, J. W. Fitzpatrick and J. G. Crock. 2000. Cadmium toxicity among wildlife in the Colorado Rocky Mountains. Nature 406: 181-183.

Legault, S. 1997. Down a slippery slope: ski resorts and their effect on ecological, social and economic health. Unpublished discussion paper, UTSB Research Inc., Banff, Alberta, Canada.

Lippman, M. 1989. Health effects of ozone: a critical review. Journal of the air and waste management association 39: 672-695.

Lloyd, H. G. 1980. The red fox. B. T. Batsford Ltd. London, UK.

Louis, S., and M. Le Berre. 1997. Visitor impact on alpine marmot foraging behaviour. Journal of Wildlife Research 2: 133-136.

Love, D. 1970. Subarctic and subalpine: where and what? Arctic and Alpine Research 2: 63-73.

Lyon, B. E. and R. D. Montgomerie. 1987. Ecological correlates of incubation feeding: a comparative study of high arctic finches. Ecology 68: 713-722.

Manuwal, D. A., M. H. Huff, M. R. Bauer, C. B. Chappell, and K. Hegstad. 1987. Summer birds of the upper subalpine zone of Mount Adams, Mount Rainier, and Mount St. Helens, Washington. Northwest Science, 61: 82-92.

Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal and demographic rescue in spatially-structured white-tailed ptarmigan populations. Condor 102, 503-516.

——, C. Doyle, F. Mueller and S. J. Hannon. 2001. Forest grouse and ptarmigan. Chapter 11 *in*: C. J. Krebs, R. Boonstra and S. Boutin, editors. Ecosystem dynamics of the Boreal Forest: The Kluane project. Oxford University Press. In press.

———, R. F. Holt and D. W. Thomas. 1993. Getting by on High: ecological energetics of arctic and alpine grouse. Pages 33-41 *in* C. Carey, G. L. Florant, B. A. Wunder, and B. Horwitz, editors. Life in the Cold: Ecological, physiological, and molecular mechanisms. Westview Press, Boulder, Colorado, USA.

————, P. B. Stacey, and C. E. Braun. 1997. Demographic rescue and maintenance of population stability in grouse — beyond metapopulations. Wildlife Biology 3: 295-296.

Medin, D. E. 1987. Breeding birds of an alpine habitat in the southern Snake Range, Nevada. Western Birds 18: 163-168.

Menoni, E., and Y. Magnani. 1998. Human disturbance of grouse in France. Grouse News 15: 4-8.

Miquet, A. 1986. Contribution a l'étude des relations entre Tetras-lyre *Tetrao tetrix* (L.) Tetraonidae et tourisme hivernal en Haute-Tarentaise. Acta Oecologia, Oecologia Applications 7: 325-355.

Nethersole-Thompson, D., and A. Watson. 1981. The Cairngorms. Melven Press, Perth, U.K.

Neuhaus, P. and B. Mainini. 1998. Reactions and adjustment of adult and young alpine marmots *Marmota marmota* to intense hiking activities. Wildlife Biology, 4: 119-123.

Norvell, J. R., and P. D. Creighton. 1990. Foraging of horned larks and water pipits in alpine communities. Journal of Field Ornithology 61: 434-440.

Noss, R. F., H.B. Quigley, M.G. Hornocker, T. Merrill, and P.C. Paquet. 1996. Conservation biology and carnivore conservation in the Rocky Mountains. Conservation Biology 10: 949-963.

Observatoire des Galliformes de Montagne. 1997. Rapport annuel de l'Observatoire des Galliformes de Montagne.

Onderka, D. K., S. A. Rawluk, and W. D. Wishart. 1988. Susceptibility of Rocky Mountain bighorn sheep and domestic sheep to pneumonia induced by bighorn and domestic livestock strains of *Pasturella hemolytica*. Canadian Journal of Veterinary Research 52: 439-444.

Pattie, D. L. and N.A.M. Verbeek. 1966. Alpine birds of the Beartooth Mountains. Condor 68: 167-176.

Piertney, S. B., A. D. C. MacColl, P. J. Bacon, and J. F. Dallas. 1998. Local genetic structure in red grouse *(Lagopus lagopus scoticus):* evidence from microsatellite DNA markers. Molecular Ecology 7: 1645-1654.

Portier, C., M. Festa-Bianchet, J.-M. Gaillard, J.T. Jorgenson and N.G. Yoccoz. 1998. Effects of density and weather on survival of bighorn sheep lambs (*Ovis canadensis*). Journal of Zoology, London 245: 271-278.

Price, L. W. 1981. Mountains and man: a study of process and environment. University of California, Berkeley, USA.

Price, M. F. and R. G. Barry. 1997. Climate change. Pages 409-445 *in* B. Messerli, and J. D. Ives, editors. Mountains of the world: a global priority. Parthenon Publishing Group, London.

Pybus, M. J., S. Groom, and W. M. Samuel. 1996. Meningeal worm in experimentally-infected bighorn and domestic sheep. Journal Wildlife Disease 32: 614-618.

Rochefort, R. M. and S.T. Gibbons. 1992. Mending the meadow: high altitude meadow restoration in Mount Rainier National Park. Restoration and Management Notes 10: 120-126.

Roland, J., N. Keyghobadi, and S. Fownes. 2000. Alpine *Parnassius* butterfly dispersal: effects of landscape and population size. Ecology 81: 1642-1653.

Saint Girons, H. 1992. Strategies reproductrices des viperidae dans les zones temperees fraiches et froides. Bulletin de la Société Zoologique de France 117: 267-278.

Shackleton, D. 1999. Hoofed mammals of British Columbia. University of British Columbia Press, Vancouver.

Shaughnessy, M. M. and T.A. O'Neil. 2001. Conservation of Biodiversity: Considerations and methods for identifying and prioritizing areas and habitats. *In* D.H. Johnson and T.A. O'Neil (Manag. Dirs.) Wildlife-Habitat Relationships in Oregon and Washington. Oregon State University Press.

Smith, A. T. 1974. The distribution and dispersal of pikas: influences of behavior and climate. Ecology 55: 1368-1376.

Smith, A. T. 1978. Comparative demography of pikas (*Ochotona*): effect of spatial and temporal age-specific mortality. Ecology 59: 133-139.

Smith, M. R., P. W. Mattocks, Jr., and K. M. Cassidy. 1997. Breeding birds of Washington State. Volume 4 *in* K. M. Cassidy, C. E. Grue, M. R. Smith, and K. M. Dvornich, editors. Washington State Gap Analysis - Final report. Seattle Audubon Society Publications in Zoology No.1, Seattle, USA.

Spalding, J. B. 1979. The aeolian ecology of White Mountain Peak, California: wind-blown insect fauna. Arctic and Alpine Research 11: 83-94.

Stabler, R. M., N. J. Kitzmiller, and C. E. Braun. 1974. Hematozoa from Colorado birds, IV. Galliformes. Journal of Parasitology 60: 536-537.

Storch, I. 1993. Patterns and strategies of winter habitat selection in alpine capercaillie. Ecography 16: 351-359.

——. 1997. The role of the metapopulation concept in conservation of European woodland grouse. Wildlife Biology 3: 272.

——, compiler. 2000. Grouse. Status Survey and Conservation Action Plan 2000-2004. WPA/Birdlife/SSC Grouse Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK and the World Pheasant Association, Reading, UK.

Suchant, R., and R. Roth. 1998. Tourism in the Black Forest - danger for the capercaillie. Grouse News 15: 13-17.

Sutherland, G. D., C. L. Gass, P. A. Thompson, and K. P. Lertzman. 1982. Feeding territoriality in migrant rufous hummingbirds: defense of yellow-bellied sapsucker *(Sphyrapicus varius)* feeding sites. Canadian Journal of Zoology 60: 2046-2050.

Sutherland, W. J. and J. D. Reynolds. 1998. Sustainable and unsustainable exploitation. Pages 90-115 *in* W. J. Sutherland, editor. Conservation science and management. Blackwell, Oxford, UK.

Taylor, K. A. 1994. Pages 165-185 *in* A Birder's Guide to Vancouver Island. Keith Taylor Birdfinding Guides, Victoria.

Thompson, D. B. A. and D. P. Whitfield. 1993. Research on mountain birds and their habitats. Scottish Birds 17: 1-8.

———, A. Watson, S. Rae, and G. Boobyer. 1996. Recent changes in breeding bird populations in the Cairngorms. Botanical Journal of Scotland 48: 99-110.

Tomback, D. F. 1998. Clark's Nutcracker (*Nucifraga columbiana*). Pages 1-24. *In:* A. Poole and F. Gill, editors, The Birds of North America, No. 331. The Academy of Natural Sciences, Philadelphia, USA.

Twining, H. 1940. Foraging behavior and survival in the Sierra Nevada rosy finch. Condor 42: 64-72.

Verbeek, N. A. M. 1967. Breeding biology and ecology of the horned lark in alpine tundra. Wilson Bulletin 79: 208-217.

———. 1970. Breeding ecology of the water pipit. Auk 87: 425-451

———. 1981. Nesting success and orientation of water pipit *Anthus spinoletta* nests. Ornis Scandinavica 12: 37-39.

Watson, A. 1979. Bird and mammal numbers in relation to human impact at ski-lifts on Scottish hills. Journal of Applied Ecology 16: 753-764.

———. 1982. Effect of human impact on ptarmigan and red grouse near ski lifts in Scotland. Page 51 *in* Annual Report of ITE for 1981, Cambridge, UK.

———. 1991. Increase of people on Cairngorm plateau following easier access. Scottish Geographical Magazine 107: 99-105.

Weaver, J.L., P.C. Paquet and L.F. Ruggiero. 1996. Resilience and conservation of large carnivores in the Rocky Mountains. Conservation Biology 10: 964-976.

Widmer, M. 1993. Breeding biology of the garden warbler *Sylvia borin* in a subalpine habitat in the central Swiss Alps. Der Ornithologische Beobachter 90: 83-115. German with English abstract.

———. 1996. Phänologie, Siedlungsdichte und Populationsökologie der Gartengrasmucke *Sylvia borin* in einem subalpinen Habitat der Zentralalpen. Journal für Ornithologie 137: 479-501.

———. 1999. Altitudinal variation of migratory traits in the garden warbler *Sylvia borin*. PhD Thesis, University of Zurich, Zurich, Switzerland.

Wiebe, K. L., and K. Martin. 1997. Effects of predation, body condition and temperature on incubation rhythms of ptarmigan. Wildlife Biology 3: 219-227.

———, and ———. 1998. Age-specific patterns of reproduction in white-tailed and willow ptarmigan *(Lagopus leucurus* and *L. lagopus)*. Ibis 140:14-24.

Woods, J.G. 1991. Ecology of a partially migratory elk population. Ph.D. Thesis. University of British Columbia, Vancouver.

Woodward, F. I. (editor). 1992. Advances in Ecological Research. Volume 22. The ecological consequence of global climate change. Academic Press, London.

Zeitler, A. and U. Glanzer. 1998. Skiing and grouse in the Bavarian Alps. Grouse News 15: 8-12.

**Web sites:**

Centre for Alpine Studies (UBC): http://www.forestry.ubc.ca/alpine/index.htm

Centre of Alpine Ecology (Italy): http://www.cealp.it/