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CHAPTER 1

The Ecological Values of Mountain Environments and Wildlife

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Abstract: Mountain ecosystems consist of alpine zones characterized by rugged, partially vegetated open terrain with snowfields and rocky ridges above montane forests. These alpine grasslands and shrublands, sub-alpine parkland and montane forest habitats are high energy environments characterized by prolonged snow cover, steep terrain, extremes of heat and cold, and intense ultraviolet radiation. With increasing elevation, time for growth and reproduction decreases, environmental conditions become harsher with increasing stochasticity; at the highest elevations, hypoxic conditions add additional energetic living costs. For plants, dispersal of pollen, seeds or ramets may be limited by topography, weather conditions and patchy habitats where access to nutrients may be limited. These factors result in short, intense growing and breeding seasons.

Only a few plants and animals live exclusively in the alpine, while many mountain species breed in both alpine and lower elevation habitats. To cope with their difficult environmental conditions, plants and wildlife living in mountain habitats have adopted a slower lifestyle where they may produce fewer offspring each year compared to populations at low elevations, but many live longer and thus have more years to breed and replace themselves. The compression of several habitat types and variable environmental conditions within small spatial areas often results in high species endemism and biodiversity in mountain areas. High elevation ecosystems are used by migrating wildlife after breeding, a time when mountain habitats offer rich food resources and when productivity in many low elevation habitats has declined. Thus, we need to include life history periods outside the breeding season to accurately evaluate the biodiversity of mountain habitats. Connectivity is a key ecological process for high elevation wildlife populations. Connectivity needs to be maintained (1) among patchy habitat islands for breeding populations, (2) along mountain corridors for north-south migrants, and also (3) between alpine and adjacent lower elevation habitats and valley bottoms for both breeding populations and migrants.

Many European and Asian mountain ecosystems are heavily altered by agriculture, forestry and intense recreational activities such as skiing developments. Although most alpine habitats in North America appear relatively intact, ecological change is also

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Christian Rixen and Antonio Rolando (Eds)

taking place over extensive areas, with some areas showing deterioration due to recreational activities, livestock grazing, mining, and airborne contaminants. Ski area development has dramatically increased in America and Europe. In addition to habitat loss from resort areas and ski pistes, high elevation habitats impacted by ski developments are vulnerable to erosion, with slow recovery of vegetation after such disturbances. On a landscape scale, developed valley bottoms constitute dispersal barriers for wildlife species with seasonal vertical movements. The cumulative impacts of ski developments and climate change increase the challenge of maintaining the key ecological processes for the persistence of flora and fauna in sensitive mountain ecosystems.

Keywords: Mountain environments, ecological processes, connectivity, endemism, human alterations, life history traits, wildlife adaptations, alpine ecology, elevational gradients and biodiversity, life history variation, alpine plants, mountain breeding vertebrates, impacts of skiing on vertebrate ecology.

THE NATURE, DISTRIBUTION AND BIODIVERSITY OF MOUNTAIN HABITATS

A mountain is a landmass arising above the general landscape that induces a change in climate that affects plant and animal life [1]. Mountain habitats include alpine treeless and partially vegetated areas at the top, the sub-alpine, which is a zone with woody shrubs, the upper limits of small trees, and montane forest comprised of open parklands and closed high elevation forest (Fig. (**1**)). Overall, mountain habitats cover ~ 40 million km^2, about 27% of the global landmass including the Antarctic continent [2]. The global alpine landmass comprises about 4 million km^2, about 30% of which is vegetated [3]. Mt. Everest (8, 848 m) on the Tibet-Nepal border is the highest elevation on earth, and Mt. Blanc (4, 810 m) and Mt. Denali (6, 194 m) are the highest peaks in Europe and North America, respectively. In Eurasia, the highest vascular plants grow at over 6100 m and the *Grandala coelicolor*, an alpine passerine, is the highest breeding bird recorded nesting up to 6, 600 m [4, 5]. Above the vegetated zone (including lichens and mosses) is the Aeolian Zone, composed of wind-blown organic matter (pollen, fungal spores, bacteria, insect bodies) that supports communities of hardy insects and invertebrates.

The word *alpine,* which comes from the Alps, 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 [6]. Several factors define the alpine zone, including elevation, aspect and high relief, but climate is probably the best determinant of where alpine zones begin [1, 3]. Temperate alpine climates are characterized by low effective moisture, prolonged snow cover, and intense ultraviolet radiation [7]. Alpine ecosystems are structurally simple with steep local gradients in snow cover and soil moisture that govern the productivity and distribution of alpine plants. Alpine plants are slow growing in soils that have developed over centuries, and many species have developed a slow life history where they are long-lived and have well-developed systems of vegetative reproduction [2, 4]. Their phenology and distribution may be governed by snow melt patterns [8]. Their recovery from disturbance and re-vegetation is usually slow (see Chapter 4 of this eBook).

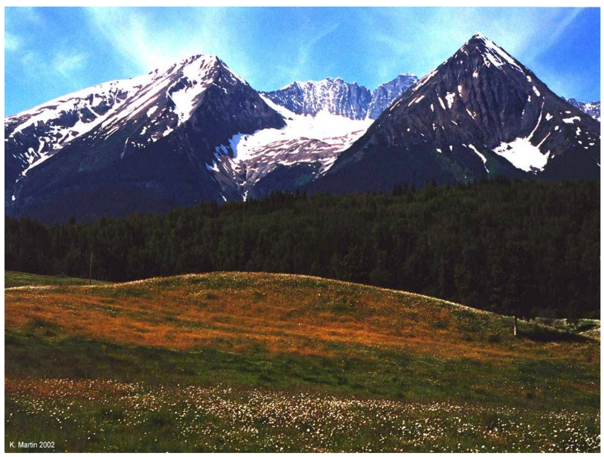

Figure 1: Hudson Bay Mountain in British Columbia, showing alpine and sub-alpine habitats above montane forest indicating the diversity of habitats in proximity along elevational gradients in mountain ecosystems (Photo by K. Martin, July, 2002).

About one third of the global mountain landmass is comprised of closed forests covering over 9 million km^2, and these mountain forests represent about 28% of the world's closed forest area [9, 10]. Topography varies from steep to gentle, and winter snow pack can range from 2 to 20 meters in gullies to exposed windswept ridges. Although the vegetation structure is relatively 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 mountain forest habitats. Globally, about 4 million km^2 of mountain forests are coniferous forest and the rest are broad leaf forests, of which about 2 million km^2 are moist tropical forests [9]. Mountain forests play vital roles in ensuring the quality and reliable quantities of fresh water flows by capturing and storing rainfall, regulating flows and reducing soil erosion and downstream sedimentation [11]. Mountain forests support exceptional levels of biodiversity and often high endemism, because as different life zones succeed one another with increasing elevation, a wide range of ecosystems are compressed into a relatively short horizontal distance [12]. Mountain forests provide important resources for local and industrial forestry, non-wood products, and hunting and gathering opportunities for mountain people. In addition, they are important sacred places, and sites for tourism and recreation [9]. Overall, mountain forests provide a wide range of benefits to both mountain people and downstream low elevation populations in terms of watershed protection and transportation infrastructure. A significant proportion of ski stations and mountain resort areas occurs in these productive mountain forest ecosystems.

Mountain habitats are essentially vertical islands. Alpine plants are constrained by their substrate and have to depend on wind, or animal dispersal to move between these discrete habitat patches. Alpine specialist animals, such as white-tailed ptarmigan (*Lagopus leucura*), alpine marmots (*Marmota marmota*) and chamoix (*Rupicapra rupicapra*) 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. A surprising number of species breed across elevation gradients from sea level to over 4000 m, and the high elevation populations for these species show strong ecological and life history variation [13, 14]. Finally a wide range of species breeding at low elevations or in northern latitudes make seasonal movements to higher elevations after the breeding season to capitalize on the late season food resources [15, 16]. In North Western North America, about one third of the ~ 590 species of vertebrate fauna regularly use high elevation sites. Thus, connectivity is a key ecological process to maintain for mountain species.

Mountain plants and animals, are well adapted for extreme environmental conditions, but they are vulnerable to anthropogenically-induced changes such as increased environmental extremes, competition from both invasive species and low elevation generalist species, increased predation pressure or unfamiliar physical barriers ([17, 18], see also Chapter 7). Thus the main ecological values of mountain plants and animals that I will cover in this chapter relate to patterns of life history variation and endemism, seasonal movements of species across elevation gradients, and the critical connectivity processes across time and space needed to maintain these levels of biodiversity. All of these entities are threatened to varying degrees by ski operations. The following chapters in this eBook cover topics related to many of these threats including habitat loss and degradation due to on-site mechanical disturbance of soil and removal or damage of vegetation, and the challenges to achieve vegetative restoration in fragile plant communities. Other chapters examine the influences on animal populations and communities due to habitat loss and degradation, the disruption of animal activities and movements, and the impacts of disturbance by skiers and the placement of physical barriers in mountain habitats. The larger issue of climate change and reliable snow cover in the European Alps, as well as many mountain areas with a significant ski industry, poses additional concerns for the persistence of alpine plant and animal communities.

ENVIRONMENTAL CONDITIONS AND WILDLIFE ADAPTATION FOR HIGH ALTITUDES

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 through the shallow soils with limited organic matter (see Chapter 3). Although alpine soils are normally cold, daily summer temperatures near the ground range from a few degrees below freezing to almost 50ºC [19, 20]. Thus, during mid day, dessication and overheating can be a problem for mountain 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). Spatial and temporal variation in resources can extend the availability of food and cover for wildlife, but accessing these temporally variable resources requires good mobility and longer movements from patchy breeding habitats to winter areas [21]. Alpine environments also show significant stochasticity in environmental conditions annually with some years of low snow cover leading to an absence of cover for sub-nivean species and, in other years, such as in el nino years in the Pacific Northwest of North America, much alpine breeding habitat can remain snow-covered for the entire season [22, 23]. With increasing elevation, time for breeding decreases and environmental stochasticity increases, and at the highest elevations, hypoxic conditions add additional energetic living costs [13, 15, 24, 25]. These factors result in short, intense breeding seasons for wildlife, and the need for seasonal movements from patchy breeding habitats to winter areas. However, there are a number of advantages species have for living and breeding in alpine environments (Table **1**).

Table 1: Advantages to Living in Alpine Habitats

1.	Extensive snow pack provides reliable sub-nivean habitats and cover for winter dormancy, hibernation and snow roosting.
2.	Windswept ridges and increasing snow level through winter provide new feeding areas temporally.
3.	Progressive snow melt in summer provides a continuing new supply of areas for germination and foraging.
4.	Lower inter- and intra-specific competition for food and growing space compared to low elevations.
5.	Low levels of parasitism and disease.
6.	For migratory animals, low elevation habitats in relatively close proximity to alpine.
7.	Thermal inversions at mid-mountain slopes may provide warmer temperatures in winter than valley bottoms for wildlife.

Mountain animals respond to living in extreme environments in several ways; they can migrate to warmer environments, hibernate or stay active all year. Animals living at high elevations have developed behavioral, morphological, and physiological adaptations to conserve energy and survive in these extreme habitats [15]. The type of adaptation may increase with increased time spent at high elevation. For example, species that use high elevation habitats for short periods may require only behavioral adjustments like moving to more sheltered sites to conserve energy [26-28]. The invertebrates, amphibians, and reptiles living in mountain environments are almost universally dark-colored. Melanism can contribute to heat absorption and help protect them against ultraviolet radiation [1, 29]. Hummingbirds exploiting the rich resources in sub-alpine meadows during migration go into night-time torpor if their energy reserves fall below a critical point [30]. With their small body size, alpine songbirds face special challenges to survive and breed in mountains as they must cope with cold temperatures and high winds as well as incubate small eggs that cool rapidly in near freezing temperatures. Alpine passerines breeding at high elevations survive well despite storms and inclement weather [14]. Nest structures in some high elevation bird populations weighed almost twice as much as those at low elevations and, presumably conferred greater insulative warmth [31, 32]. Mountain songbirds may increase their parental care to warm and feed their nestlings [28, 33].

With less vegetative cover for concealment, many alpine mammals and birds have developed cryptic appearances and behaviours to enhance blending into the landscape. Ptarmigan are renowned for their cryptic plumage, but larger mammals such as bighorn sheep (*Ovis canadensis*) and coyotes (*Canis latrans*) also blend exceptionally well in these open landscapes. Mountain animals such as marmots, pika and ptarmigan have territorial and social contact calls that are difficult to localize, which may reduce the risk of their being detected by predators when calling. Animals living at high elevations increase insulation by developing fat deposits or thicker fur during winter, as well as using snow roosts or burrows during storms or periods of cold weather (Fig. (**2**)). True alpine species may

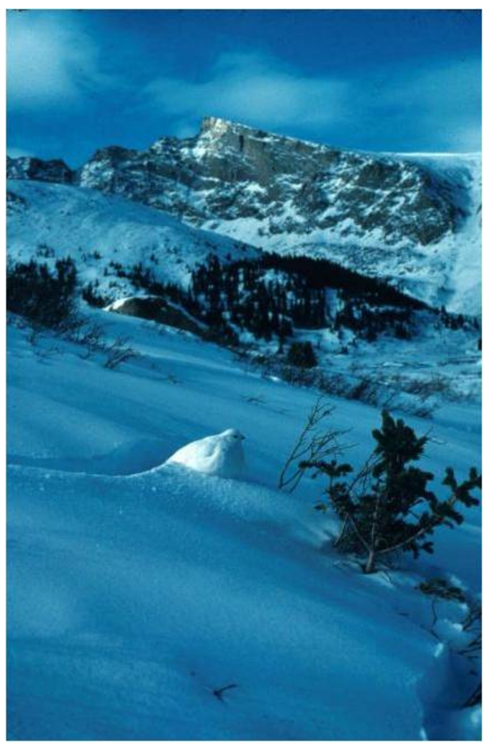

Figure 2: Only a few vertebrates remain in their alpine sky islands year round like this white-tailed ptarmigan in its winter habitat at Guanella Pass, Colorado, USA. Mt. Evans, one of their breeding habitats is shown in the background (Photo by K. Martin, January 1988).

develop structural adaptations. Alpine finches show ecological and morphological differentiation across an elevational gradient in the Himalayas with the heaviest species occupying the highest elevations [27, 34, 35]. These alpine passerines have long pointed wings for efficient flight performance in strong and variable winds [5]. Finches and chats at the highest elevations have square-ended or shallow forked tails for flight stability in wind, and elongated hind toes for grasping during ground foraging. Winds may pose problems for smaller animals, but larger animals such as raptors use wind to remain aloft and glide efficiently. Species living at the highest elevations for extended periods make biochemical adjustments such as increasing their blood hematocrit concentrations, including tropical birds that move to higher elevations in winter [25, 36, 37]. In some small mammals, life at high elevation is facilitated with genetic adaptations [38].

LIFE IS SLOW ON THE MOUNTAIN TOPS

The reduced time for breeding within a season may alter life history traits. Generally, vertebrate species living at high elevations exhibit lifestyles whereby they have slower development and lower annual fecundity (Table **2**). For some species, these traits are accompanied by longer life spans, differences in body size or shape and more developed social behaviours. Food supplies for animals in mountain habitats in summer are plentiful generally, but of short duration in a specific location, but receding snowfields in summer continually provide new foraging areas (Fig. (**3**) [22, 39]). Most alpine animals are both granivorous and insectivorous, and often forage on chilled and dead wind-blown arthropods deposited on snowfields [40, 41].

Poikilothermic (cold-blooded) animals such as frogs, salamanders and snakes have special problems moving and reproducing in cold climates because the low alpine 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 [29], in contrast to lower elevation individuals that usually achieve full maturity in their first year. In the European Alps, all three reptiles, green lizard (*Lacerta vivipara*), common viper (*Vipera berus*) and blind-worm (*Anguis fragilis*) are viviparous (bear live young). Although reptile eggs normally can not develop and hatch in such cold climates,

Figure 3: Mountain habitats exhibit exceptional seasonality with delayed snow melt in May, standard growing and breeding season conditions in June and a profusion of alpine vegetation in July that attracts vertebrates and hikers to move up to the alpine in late summer. This alpine prairie occurs on the Hudson Bay Mountain ski area, Smithers, British Columbia, Canada (Photos by K. Martin).

when 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. Snakes in the European Alps show delayed sexual maturity and reproduce every two to four years in the alpine, rather than annually as found in low elevation populations [42, 43].

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 [15]. Of these, only the alpine ptarmigan are year-round residents. Population densities of species that breed across a range of elevations might be expected to decrease with increasing elevation, but this was not found for garden warblers (*Sylvia borin*) [31]. In Europe and Asia, black redstarts (*Phoenicuros ochruros*), European skylarks *Alauda arvensis* and Himalayan chats increased in density with elevation [34, 44, 45].

A number of birds breeding in mountain habitats are able to do so because they shift to a slower life history with increasing elevation [13, 14, 31]. Mountain breeding songbirds have only about 50% as much time to breed as lower elevation populations because onset of breeding is delayed by several weeks at high elevation, and high elevation songbirds in Europe and North America do not extend their egg laying period beyond that of low elevation populations. Most species breeding across elevation gradients produced fewer broods annually at higher elevations, with generally only a single brood at high elevations [28, 46, 47]. At high elevations, White-tailed ptarmigan (*Lagopus leucura*), showed slower laying rates, smaller clutches, longer incubation periods with higher reproductive failure and a larger body size compared to their arctic breeding conspecifics and congenors, willow ptarmigan (*L. lagopus*) [48-51]. Both alpine specialist and generalist breeding birds produced fewer young annually, but their annual survival was 10 to 20% higher (Fig. (**4**)). It has not been established whether the mechanisms underlying this life history variation represent genetic differences or are achieved by phenotypic plasticity.

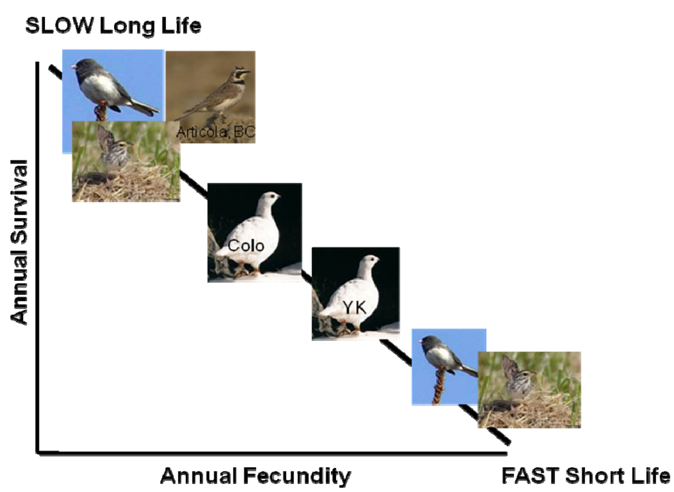

Figure 4: Life history varies within species and is slow on mountain tops. Conspecific populations of birds living at high elevations have lower annual production of offspring, but they live longer and thus have more time to replace themselves. In some cases, these slow lifestyle populations are stable while the low elevation populations are declining such as the horned lark, or have been extirpated as in the case of the black grouse in Central Europe.

A study of golden-mantled ground squirrels (*Spermophilus lateralis*) across five elevations in the Sierra Nevada in California showed delayed age of maturity, lower litter size and greater survivorship of females with increasing elevation [52]. At high elevations, Columbian ground squirrels (*S. columbianus*) have lower litter size, lower female body weight, lower proportion of young females breeding, and higher adult survival relative to low elevation populations. Some of these within-species differences (*e.g.*, litter size and proportion of young females with litters), disappeared when high elevation populations were food-supplemented suggesting that ground squirrel populations showed a phenotypically plastic life history response to variation in food availability with elevation [53, 54]. 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 [55-58].

In summary, there may be high ecological costs to living 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 inter-specific competition than wildlife occupying lower elevation habitat types. To cope with difficult environmental conditions at high elevations, some mountain species have adopted a slower lifestyle where they produce fewer offspring annually compared to those at low elevations, but they live longer and thus have more years to breed and replace themselves (Summary given in Table **2**). Other species of birds and mammals may also have differentiated high elevation ecotypes or subspecies yet to be discovered. It is important to know about the nature of wildlife adaptations to living in high elevation environments as the adverse impacts of ski operations on populations such as increased mortality due to ski cables or disruption of their snow burrowing behaviours or foraging activities by skiers will have a greater impact on animal populations with slow lifestyles than those that depend less on longevity to replace themselves. Thus, we cannot assume that studies on animals or plants are directly comparable for low and high elevation populations.

Seasonal migration to mountain habitats: From late summer to fall, alpine areas support a high diversity and abundance of invertebrates, birds, and mammals that move up from lower elevations, or down from higher latitudes. In North America,

Table 2: Ecological Values and Processes Associated with Plants and Animals Living in Mountain Environments

	Plants	**Animals**
Ecological Traits	Cushion plants Vegetative reproduction Limited number of pollinators	Larger body size Good dispersal abilities Flexible breeding schedules
Connectivity	Seed and ramet dispersal	Need to disperse to winter areas to recruit to new breeding sites
Life History Strategy for both specialists and generalist alpine species	Long lived, mostly perennials High reliance on vegetative reproduction	Larger body size Shift to slower lifestyle
Threats due to Skiing	Habitat loss due to ski pistes and structures Sensitive to soil disturbance and compaction Slow to recover from disturbances	Habitat loss Seasonal movements more difficult Disturbance/harassment in winter habitat Mortality due to infrastructures and predation
Threats due to Climate Change	Habitat loss/degradation Less reliable winter conditions; Mortality due to thaw/freeze events	Habitat loss with winter warming Tree and shrub line will rise Ice/storm events increase mortality
Other Threats	Upward range shifts of invasive species and competitors	Upward range shifts of invasive species and competitors

about 240 species of birds, and many mammals and invertebrates make seasonal migrations to use alpine, sub-alpine and montane habitats in late summer as stopovers for replenishing body reserves. [1, 59, 60]. However, the importance of this phenomenon and the key ecological processes has received little study, especially in relation to ski operations. About 80% of the 114 bird species observed from early August to October during a three year field study in British Columbia, Canada did not breed at high elevation [16]. Some species were 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 raptors such as sharp-shinned hawks (*Accipiter striatus*) and northern goshawks (*Accipiter gentilis*). A high proportion of birds arriving in the alpine were probably elevational migrants of local origin such as some forest birds, (*e.g.*, nuthatches and siskins), that moved up the mountain to track emerging food resources (insects/ flower/ fruit) from snow melt and green-up in late summer. The proximity of mountain habitats to forest, grasslands, shrub steppe or coastal habitats at lower elevations means that animals can move quickly between these habitats (Fig. (**5**)). Rufous hummingbirds (*Selashorus* *rufus*) are generally the first avian migrants to move up to sub-alpine meadows in late summer and defend territories around flower patches [61, 62]. From mid August to early September, alpine grasslands support large numbers of grasshoppers that are eaten by kestrels (*Falco sparverius*), and songbirds in both Europe and North America [22]. Migrating raptors use the open mountain terrain to hunt for landbirds and small mammals, often using updrafts along cliff faces and ridges. The use of high elevation sites as migration stopover habitats may be increasing in importance especially where late summer fruits in the sub-alpine such as huckleberry (*Vaccinium deliciosum*), crowberry (*Empetrum nigrum*), and bearberry (*Arctostaphylos uva-ursi*) are available. Their availability may offset some of the loss of traditionally used low elevation migration stopover habitats. Ungulates and carnivores also make seasonal movements up to alpine areas in late summer and fall. With the continued expansion of large mountain resort areas, there has been a strong increase in 'shoulder season' recreation activities such as mountain biking on or near ski pistes that can lead to conflicts between recreational activities and fall feeding activities of these migrant wildlife species. At Whistler and Blackcomb ski resort, British Columbia, bears feeding in the late summer vegetation in subalpine meadows have been disturbed and sometimes hit by mountain bikers.

Figure 5: Seasonal connectivity. Many species of vertebrates migrate upslope or from higher latitudes for a period of several months in late summer and autumn to capitalize on the abundant food resources. A few species migrate up to the treeline in winter. Recreational and ski activities can negatively impact these seasonal movements of medium-sized and large vertebrates (Photo by Steve Ogle).

Winter Residents: In North America, relatively few wildlife species winter in alpine areas, and fewer still remain active in winter. Some birds, including white-tailed ptarmigan, raven, and rosy finches 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 [63]. Gray jay (*Perisoreus canadensis*), raven, Clark's nutcracker (*Nucifraga columbiana*), and hardy songbirds like golden-crowned kinglets (*Regulus satrapa*) and dark-eyed juncos (*Junco hyemalis*) in North America use tree islands in sub-alpine parklands in winter. Mammals using alpine and sub-alpine habitats in winter include pika, mountain caribou (*Rangifer tarandus*), and mountain goat (*Oreamnos americanus*) and their predators, fox, coyote, pine marten (*Martes americana*), wolverine (*Gulo gulo*), lynx (*Lynx canadensis*), bobcat (*Lynx rufus*), and mountain lion (*Felis concolor*) hunt along or above the treeline. White-tailed jackrabbits (*Lepus townsendii*) winter at the interface of wind swept ridges and the krummholz [64]. For marmots and ground squirrels that hibernate at high elevations, their choice of burrow and amount of snow cover can be crucial to overwinter survival [56-58]. Pika, weasel and vole remain active in the sub-nivean layer where they have temporary reprieve from predators and winter storms.

Winter may be a period of great sensitivity, with human disturbances from both nordic and alpine skiing possibly causing the most adverse impacts on wildlife [65]. In winter, many grouse and ungulates occur in social groups and live at about the same elevational range as alpine and Nordic ski facilities. On Vancouver Island, British Columbia (Canada), for example, white-tailed ptarmigan move from an average summer elevation of 1676 m down to treeline (1372 m) in winter [22], while sooty grouse (*Dendragapus fuliginosus*) move up to the treeline elevation [66]. In Bavaria, black grouse (*Tetrao tetrix*) are largely restricted to using treeline islands in the sub-alpine in winter where they are hindered from feeding during the day by disturbance from skiers [67]. The soft snow used by mammals and grouse for snow burrows to take refuge from winter storms, is also sought by back-country skiers (see Chapter 8). In addition, mortality due to collision with ski cables can result in strong negative impacts on some alpine winter resident birds (see Chapter 7).

Increases in recreational use of high elevation areas can result in increased food availability for generalist predators and also human activities at lower elevations may influence ecological processes in the alpine. High elevation habitats are generally unsuitable for corvids such as crows, jays or choughs, but populations can persist if there are dwellings or dumps nearby [68]. In winter, the alpine chough (*Pyrrhocorax graculus*) roosts in holes in high cliffs, but individuals usually make daily elevational movements of over 10 kilometers to the snow free valleys. However, choughs near ski-resort towns remain at high altitude and feed on tourist scraps (see Chapter 6). Over-winter survival of generalist predators may also be improved by road-kills, dumps in adjacent urban areas, or from feeding from homes in the montane forest. When these anthropogenic food supplies are available, generalist predators are less dependent on traditional prey year-round to survive. Densities of foxes and corvids tend to be higher close to ski resorts, which may thus increase the predation pressure on the birds [69]. If predator densities near ski stations are higher, prey species breeding in the proximity will in some cases be negatively impacted. In the Cairngorm Mountains in Scotland, ptarmigan densities were lower and were associated with an increased predation rates on nests, young or adults near ski resorts compared to areas less frequented by humans [70, 71]. The cumulative impacts from ski facilities and the activities of skiers can have serious adverse impacts on a range of taxa that are observed over considerable distances in all seasons. Generally, this topic is not well studied, but some of the ecological impacts are covered in detail in succeeding chapters in this eBook.

In summary, about one third of the vertebrate fauna in western North America use mountain habitats at some critical period in their life history. It is difficult to generalize about the relative reproductive success and survival for wildlife species living at high and low elevations, because there are so few studies of the ecology, behaviour, and life history of the upper elevational ranges. The few studies done suggest there is greater local adaptation and life history diversity than previously realized. The period of highest biodiversity in mountain habitats is between late July and October. To accurately characterize the biodiversity of mountain ecosystems, we need to consider life history periods outside the breeding season. Ski resorts and their associated activities during winter and fall can adversely impact the foraging activities of winter resident species and fall migrants by restricting the areas or times when wildlife can feed without harassment or stress.

For some species, survival is reduced or population density is also reduced near ski resorts, but for most species, the potential impacts have not been studied.

CONNECTIVITY IN MOUNTAIN HABITATS

Connectivity is a key ecological process for high elevation plant and animal populations across all seasons. Connectivity needs to be maintained (1) among populations breeding in patchy alpine habitats, (2) along mountain corridors for north-south migrants, and also for (3) elevational migration between high elevations and adjacent lower elevation habitats.

Demographic connectivity across patchy habitats. – The ability of pollen, seeds or individuals to achieve dispersal and recruitment are crucial requirements for the persistence of mountain species given the patchy nature of high elevation habitats. Generally, alpine plants are long-lived and rely heavily on clonal growth to maintain populations. Dispersal of pollen and seeds by either wind or animals can be critical to colonize new alpine patches or to restore damaged vegetation. However, colonization can be a slow process as the number of pollinators generally decreases with elevation, given the colder environmental conditions and the glow growth [3]. Restoration and re-vegation using clonal growth can be done, but is also slow and works better for smaller areas of disturbance ([72], see also Chapters 9 and 10).

Despite the tendency for small population sizes, animals adapted to live in naturally fragmented alpine habitats may generally have well developed dispersal abilities. The enabling factors for this extensive external recruitment appear to be low costs to dispersal and low benefits to philopatry. Populations of white-tailed ptarmigan breeding in highly fragmented alpine habitats, with corresponding small populations, in the Rocky Mountains of Colorado, USA showed dramatic variation in offspring production and survival of adults across years and sites, yet breeding populations remained relatively stable [21, 49]. Although population simulation models predicted that all populations should go extinct in 2 to 10 years all have persisted for at least 4 to 5 decades. Local populations were able to avoid extinction due to external recruitment; about 95% of females and 75% of males recruiting to alpine sites did not originate from any of the study populations. On

Vancouver Island, British Columbia, there was little genetic differentiation observed for ptarmigan breeding in highly fragmented and stochastic coastal alpine habitats, indicating there was extensive dispersal of alleles at a landscape scale [73]. For small populations in stochastic environments, maintaining connectivity between populations is crucial and can be achieved as long as there is a balance of populations producing recruits in reasonable proximity to populations requiring rescue [21, 48-50]. However, some mountain vertebrates are not able to disperse readily between unconnected patches. The development of ski-pistes was found to limit movements for small mammals that are reluctant to cross open spaces (Fig. (**6**), [74], see also Chapter 6). When ski activities are combined with other sources of habitat loss and fragmentation at larger spatial scales, population sizes become smaller and genetic diversity is reduced as found for mountain forest grouse in central Europe [75].

Figure 6: Development in narrow valley bottoms associated with skiing, other recreations and transportation activities can impede animal movement, thus fragmenting wildlife populations at the landscape scale (Photo by Amanda Adams, Canmore near Banff National Park, Alberta, Canada. June, 2010).

Latitudinal migration along mountain corridors and elevational migrants - 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 [16]. Stopovers in mountain areas in spring occur to a much lesser extent as these areas are generally fully snow-covered during spring migration. 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.

The issue of connectivity between high and low elevation habitats is an important biological and management question. A high proportion of habitats in parks in the Rocky Mountains of North America are at high elevation, and most parks do not contain year-round habitat requirements for wildlife species such as migratory elk (*Cervus elaphus*) in Banff National Park (Alberta, Canada) [76, 77]. For alpine residents, we need to ensure that connectivity is maintained from alpine habitats to adjacent lower elevation forests and valley bottoms. Since many alpine areas are not continuous, larger area sensitive mammals in North America and Europe often require access to valley bottoms to move between mountain chains. In North America, urban areas and transportation infrastructure in valley bottoms generally interrupt wildlife movements, act as a dispersal barrier, restrict access to seasonally-used habitats and can permanently sub-divide populations of large ungulates and predators (Fig. (**7**), [17]).

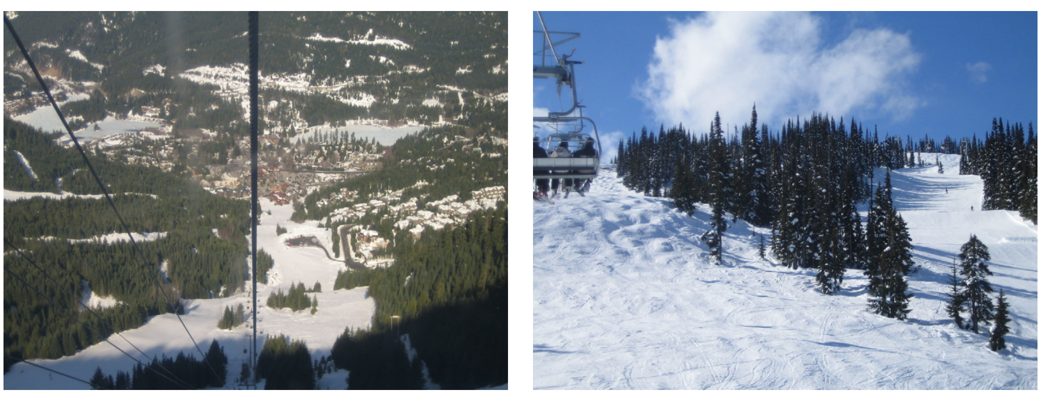

Figure 7: Smaller scale cutting for ski runs can impede wildlife movements and reduce the quality of denning areas for mountain mammals. Whistler, British Columbia, Canada (Photos by Kathy Martin, March 2011).

The most severe wildlife-human conflicts occur in mountain landscapes with narrow valleys that are densely settled or developed. Barriers to seasonal movements or population dispersal pose a serious problem in mountain systems such as Banff

National Park, Canada where urban developments, major highways and railways in the narrow Bow Valley have greatly impeded movements of large mammals and fragmented their populations causing increased mortality due to collisions with motor vehicles or trains [78]. Even if infrastructures are designed to facilitate dispersal movements, species can vary in their willingness to cross such dispersal barriers (Fig. (**8**), [77, 79]). Mountain passes are also important for seasonal access or population connectivity, and these tend to be where roads, trails and recreational huts are situated. Determining the ecological value of the alpine as migration habitat and minimizing interruptions of wildlife movements in mountains are high priorities for additional research on the ecological impacts of ski areas.

Figure 8: The TransCanada Highway, a railway and the town of Banff are all situated in the narrow valley bottom of the Bow Valley in Alberta. These structures have been found to impede the movements of large ungulates and carnivores. The wildlife connectors shown here have been installed over the highway to reduce mortality and facilitate movements of animals across the valley. Banff-Jasper Highway, Alberta, Canada (Photo by Kathy Martin, March 2011).

UPWARD SHIFTING OF SPECIES ELEVATIONAL DISTRIBUTIONS

Some wildlife species that formerly used habitats over a broad range of elevations are becoming restricted to the upper elevations of their historical range. ‘Upward shifting’ is a well advanced phenomenon in central Europe where 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 (*Lyrurus tetrix*) in central Europe are now 'de facto' sub-alpine parkland species due to the current unsuitability of their traditional low elevation habitats [67, 75]. In northern Italy, skylarks and golden eagles (*Aquila chrysaetos*) are largely confined in the Alps [45]. As well, wolves and brown bears (*Ursis arctos*) in Europe are largely restricted to high latitudes and mountain habitats [80]. Many of these 'upshifted' species are now endangered, because they regularly experience total reproductive failure due to reduced cover and the generally high numbers of predators in their high elevation habitats and possibly due to the lack of recruitment of individuals from lower elevation populations [75]. Predation risk might also be increasing at some high elevation locations if generalist predator densities have increased as a result of human presence [69, 70]. The upshifting of species ranges is an ecological process that also has begun in western North America, where many low elevation coniferous forests have been converted to intensive agricultural, industrial or urban areas and, many low elevation wetlands have disappeared [81, 82]. Hence, wildlife species that traditionally occupied a broad elevational range of habitats have also experienced significant range reduction, accompanied with an 'upward shift', including such species as white-tailed jackrabbit, western toad (*Bufo boreas*), other amphibians, sooty grouse, and ruffed grouse (*Bonasa umbellus*). For example, sooty grouse numbers have declined in many low elevation areas of Washington and Oregon, while the high elevation populations remain unchanged [83]. Medium- and large-sized predators such as grizzly, wolf or lynx that do not persist easily near urban areas have also moved higher. For most of the large predators and ungulates, the 'upward shift' in population distribution is facilitated by greater conflicts with humans as well as habitat loss at low elevations.

For those wildlife species living at higher elevations, we need to determine which species have experienced the largest elevational increases and whether their populations appear in difficulty. As discussed earlier, there are potential increased energetic costs of living at higher elevations as well as the impacts on reproductive success and population viability as the frequency and severity of stochastic events increase [13, 21]. For large carnivores in both North America and Europe, the retreat to high elevation habitat patches results in populations being more fragmented than formerly by anthropogenic barriers [17, 84]. After the low elevation population segment is extirpated, the risks to population viability of wildlife species in spatially separated high elevation 'islands' will increase due to habitat fragmentation and reduced effective population size, especially in areas with a high density of large ski resorts. The presence of other winter sport activities such as Nordic skiing, snowmobiling and dog sledding in proximity to intensive alpine ski stations increases the cumulative impacts to mountain species and over a larger spatial scale. Disturbance due to skier activities represents a serious additional threat especially to populations already in trouble from other stressors (see Chapters 2 and 8, [85]).

OTHER CHANGES IN ECOLOGICAL PROCESSES AND RESEARCH NEEDS AT HIGH ELEVATIONS

In the past three decades, there has been a dramatic increase in the number and ecological footprint of alpine and Nordic ski stations, and in the use of helicopters to access remote areas for skiing, fishing, and hiking. Helicopter-supported activities do not result in many visits to each mountain, but they increase dramatically the overall size of area impacted especially for area sensitive species like mountain goats or chamois [85, 86]. The increased use of alpine facilities in fall, particularly with late summer hiking and mountain biking, results in conflicts with the seasonal movements of wildlife. Careful evaluation of habitat use is needed and the seasonal wildlife travel corridors need to be determined in advance of designing and approving new ski developments or expanding existing operations [87]. Reviews of proposed new housing and other amenity developments or expansions of ski resort areas should consider off-site impacts. Potential impacts should be evaluated at a sufficiently large scale to include connectivity issues discussed earlier for maintaining viable populations of mountain flora and fauna [88]. Proposed mountain recreational developments should demonstrate that they have allowed for the maintenance of the usual ecological and connectivity processes.

Alpine and sub-alpine areas have increased in value as wildlife habitat, given habitat loss and changes in ecological processes at low elevations. Research is needed to determine the important ecological processes and habitat functions required by mountain plants and animals. Life history studies are needed for alpine generalist species that are experiencing extensive habitat loss at low elevations. Most research for alpine fauna has been done in summer and, thus our knowledge of their use of mountain areas in other seasons is limited. 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.

Increases in predator density or the amount of time predators spend in the alpine could significantly increase the risk of predation for alpine and sub-alpine species, as well as for those 'upward shifted' elevational generalist species. Better understanding of the possible factors that increase generalist predator densities in or near high elevation areas, and whether these increases significantly impact alpine wildlife populations. Thus field research is needed on how to maintain the normal balance of predator-prey dynamics in mountain areas in proximity to ski pistes and other structures associated with ski operations to minimize the potential negative impacts on survival for alpine plants and wildlife.

Research is needed on the influence of montane forest cutting on the distribution and abundance of generalist predators, and the consequent impacts on survival and reproduction of plants and wildlife in adjacent sub-alpine and alpine habitats.

Most urgently, research is needed to improve predictions on how wildlife species will cope with changing climatic and environmental conditions ([89], see also Chapter 2). To detect and predict the ecological effects of global climate change, it will be crucial to establish and maintain existing long-term mountain habitat and species monitoring programs similar to programs in the Austrian Alps [90], northern Finland [91], or in the Rocky Mountains [92]. Plants and animals living in alpine patches that are shrinking will have smaller populations and be required to disperse longer distances to other alpine patches, or pay the consequences of not dispersing [21, 93]. Although some subalpine species will experience an increase in habitat, many alpine species will need to cope with a reduction and fragmentation of their habitat supply, while also experiencing increased competition from species invading and upshifting from lower elevations [18].

In sum, alpine and sub-alpine areas have increased in value as wildlife habitat, given habitat loss and changes in ecological processes such as climate change and upshifting of invasive and competitive species from low elevations. With the limited data for baseline conditions, we are poorly positioned to detect changes in ecological processes or population declines at an early stage, especially if processes such as predation are shifting at large cross-habitat scales. Research on most of these issues is limited, especially in North America. The following chapters focus on studies conducted in the European Alps, and are excellent examples of the kinds of research needed for the management and mitigation of impacts from recreational activities in mountain areas. They develop in detail the chronic and acute problems experienced by soils, habitats, plants and animals associated with the direct and indirect impacts from alpine and Nordic ski operations and associated synergistic interactions with climate change processes.

CONFLICT OF INTEREST

The author confirms that this article content has no conflict of interest.

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