White-tailed Ptarmigan (*Lagopus leucura*): A Technical Conservation Assessment

Prepared for the USDA Forest Service,
Rocky Mountain Region,
Species Conservation Project

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Richard W. Hoffman earned his B. Sc. and M. Sc. Degrees in wildlife biology from Colorado State University. He subsequently worked for the Colorado Division of Wildlife for over 30 years as an avian researcher specializing in upland game birds. He has conducted research on population dynamics, habitat relationships, and behavior of white-tailed ptarmigan, blue grouse, greater prairie-chickens, Columbian sharp-tailed grouse, and wild turkey. In retirement, he continues to work on projects involving white-tailed ptarmigan and Columbian sharp-tailed grouse.

COVER PHOTO CREDIT

Photograph by Mark Parchman of male white-tailed ptarmigan in fall plumage, used with permission.

SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF THE WHITE-TAILED PTARMIGAN

Status

The white-tailed ptarmigan (*Lagopus leucura*) is endemic to alpine regions of western North America. Except for several transplants into previously unoccupied habitats, the distribution and abundance of this alpine grouse have remained relatively unchanged. Although it is not federally listed as threatened or endangered in any portion of its range, the white-tailed ptarmigan is listed as a sensitive species within the USDA. Forest Service (USFS) Rocky Mountain Region (Region 2), where it is found in suitable habitats throughout Colorado and in the Snowy Range of southern Wyoming. Colorado supports the largest population of white-tailed ptarmigan and greatest expanse of suitable habitat in the United States outside of Alaska. Approximately 84 percent of the occupied habitat in Region 2 is administered by the USFS.

Primary Threats

The greatest threat to the long-term survival of ptarmigan populations in Region 2 is global climate change, which may lead to a gradual loss of alpine habitats as the treeline moves upward in response to large-scale atmospheric temperature changes. More immediate and localized threats include grazing, mining, water development, and recreation. While alpine ecosystems are hardy and resilient to natural environmental factors, they are particularly vulnerable to human-related disturbances and may require decades, if not centuries, to recover from such disturbances. Although substantial progress has been achieved in developing techniques to restore damaged alpine landscapes, this technology is still not capable of restoring alpine plant communities to their pre-disturbance condition.

The single most important feature of habitats used by ptarmigan in Region 2 is the presence of willow (*Salix* spp.), which is their primary food source from late fall through spring. Any activity that reduces the distribution and abundance of willow will likely have negative consequences to ptarmigan.

Primary Conservation Elements, Management Implications and Considerations

The primary information needed for effective conservation of white-tailed ptarmigan in Region 2 is a clearer understanding of how the species responds to alterations in habitat and changes in environmental conditions. The natural processes that perpetuate alpine ecosystems are still intact. Consequently, human intervention is not necessary other than to insure that these natural processes are not disrupted. The key to the successful management of ptarmigan populations and the alpine ecosystems upon which they rely is protection – protection against over-use due to grazing, recreation (including hunting), mining, and development, and protection from environmental perturbations that contribute to global climate change, pollution, and depletion of the ozone layer. In formulating management strategies, it is essential to account for the cumulative impacts that human activities and climate change have on ptarmigan and the alpine environment.

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INTRODUCTION

This conservation assessment is one of many being produced to support the Species Conservation Project for the USDA Forest Service (USFS) Rocky Mountain Region (Region 2). The white-tailed ptarmigan (*Lagopus leucura*) is the focus of an assessment because it is classified as a sensitive species in Region 2 due to its limited distribution and nearly complete dependence on alpine habitats (USDA Forest Service 2003a). It is one of the few year-round residents of the alpine and is arguably the most important indicator species of the health of this ecosystem (Braun et al. 1993). Even though populations of white-tailed ptarmigan have remained stable in Region 2 and are hunted in Colorado, their reliance on alpine environments makes them especially susceptible to disturbances and development.

This assessment addresses the biology of white-tailed ptarmigan throughout its range, but in particular Region 2. Much of the understanding of the biology of this species originates from studies conducted within Region 2. Therefore, the information presented in this assessment is highly specific to Region 2.

Goal

Species conservation assessments produced as part of the Species Conservation Project are designed to provide land managers, biologists, and the public with a comprehensive discussion of the biology, ecology, conservation status, and management requirements of certain species based on current scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The ultimate purpose of the assessment is to provide managers with the ecological framework upon which to formulate sound decisions. The assessment identifies threats to the species and the implications of these threats if they are left unchecked. It cites previously published recommendations and examines the success or failure of those recommendations that have been implemented. Additionally, the assessment provides management strategies not previously proposed elsewhere along with insight into the consequences of changes in the environment that result from management (i.e., management implications).

Scope

The assessment examines the biology, ecology, conservation status, and management requirements of white-tailed ptarmigan with specific reference to the geographic and ecological characteristics of USFS Rocky Mountain Region (**Figure 1**). There is a limited amount of information on white-tailed ptarmigan outside of Region 2. Where this information is used in the assessment, it is clarified in the ecological and social context of the southern Rocky Mountains. Also, the distinction is made between information collected from areas where white-tailed ptarmigan coexist with rock (*Lagopus muta*) and/or willow (*L. lagopus*) ptarmigan and where they occur allopatrically. This assessment is concerned with the reproductive behavior, population dynamics, habitat requirements, and other characteristics of white-tailed ptarmigan in the context of the current environment rather than under historical conditions. The evolutionary environment of the species is addressed in the assessment and placed in context with the current environment. However, it is clear from this analysis that little has changed in the status, distribution, and general ecology of the white-tailed ptarmigan in recent history.

Data Used to Produce This Assessment

In producing this assessment, information was gathered from peer-reviewed sources, theses, dissertations, and agency and university technical reports. Non-refereed information was used where this information was considered reliable and necessary to fill knowledge gaps; the nature of this information is clearly acknowledged and was interpreted with caution. Not all publications on white-tailed ptarmigan were referenced in this assessment, nor were all published materials considered equally reliable. Several publications contained redundant information; therefore, it was unnecessary to cite them all. Even peer-reviewed literature has its strengths and weaknesses. If new information refutes previously published data, the discrepancies were duly noted. In addition, the strength of evidence for particular ideas was evaluated, and alternative explanations were provided when appropriate.

The first major investigation of white-tailed ptarmigan was conducted in the mid-1950's. Although the study involved some field work in British Columbia

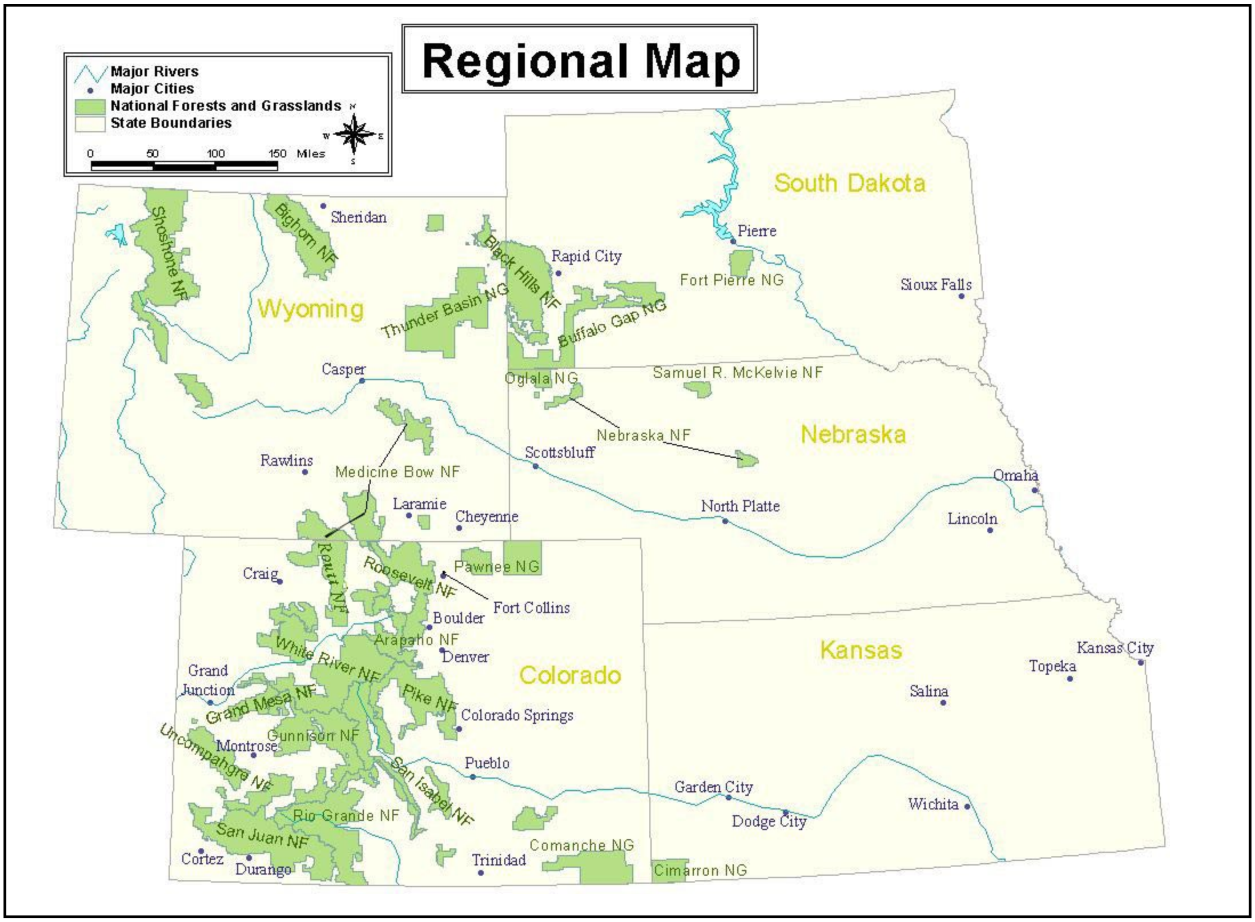

Table 1. National forests and grasslands of USDA Forest Service Rocky Mountain Region.

and Alaska, it was mainly a review of the distribution and general life history of the three species of ptarmigan in North America. The first major field investigation to focus specifically on white-tailed ptarmigan was conducted in Glacier National Park, Montana during the late 1950's and early 1960's. Studies of the population dynamics and habitat relationships of white-tailed ptarmigan were initiated in Colorado in 1966. Since then, studies in Colorado have focused on nearly every aspect of the ecology of this species, including 40 years of continuous population monitoring at Mt. Evans (Arapaho National Forest). These studies have produced more than 75 percent of the published and unpublished literature that exists on white-tailed ptarmigan. Other sources of information include studies conducted in the northern Rocky Mountains in Alberta in the 1970's and 1980's, and studies on introduced populations in the Sierra Nevada Mountains in California during the late 1980's and early 1990's. Most recently, population studies were initiated in British Columbia. No studies have been conducted in Wyoming or Washington other than general monitoring and surveys to determine presence or absence.

Users of this assessment should be aware that there is a dearth of published literature on white-tailed ptarmigan compared to other species of grouse. Storch (2000) places the number of scientific and semi-scientific publications on white-tailed ptarmigan at about 175. Of 17 grouse species listed by Storch (2000), the white-tailed ptarmigan ranked 13th in available publications. Users also should be aware that much of the published information on white-tailed ptarmigan originates from descriptive rather than experimental studies. Only recently have experimental studies been designed and conducted on this species. Despite the lack of well-executed experiments, alternative approaches such as modeling, critical assessment of observations (i.e., descriptive studies), and inferences have contributed greatly to the understanding of the ecology of white-tailed ptarmigan.

Publication of Assessment on the World Wide Web

To facilitate use of species conservation assessments produced by the Species Conservation

Project, they are being published on the USFS Region 2 World Wide Web site at http://www.fs.fed.us/r2/projects/scp/assessments/index.shtml. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. Web publication also makes future revisions and inclusion of new information easier.

Peer Review

Assessments developed for the Species Conservation Project have been peer reviewed prior to their release on the Web. This report was reviewed through a process administered by the Society for Conservation Biology, which selected two recognized experts to provide critical analysis of the manuscript. Peer review was designed to improve the quality of communication and to increase the rigor of the assessment.

MANAGEMENT STATUS AND NATURAL HISTORY

Management Status

The white-tailed ptarmigan is not federally threatened or endangered in any portion of its range (Storch 2000, Schroeder et al. 2004), nor is it considered a bird of conservation concern by the U.S. Fish and Wildlife Service (U.S. Department of Interior 2002). However, it is considered endangered in New Mexico (Hubbard and Eley 1985). The subspecies endemic to Vancouver Island (*Lagopus leucurus saxatilis*) was blue-listed (status S3: vulnerable) in 1992 by the British Columbia Conservation Data Centre because of its small population size, restricted range, and potential susceptibility to anthropogenic and natural disasters (Fraser et al. 1999, Martin et al. 2004). The white-tailed ptarmigan is listed as a Sensitive Species by Region 2 of the U.S. Forest Service (USDA Forest Service 2003a) and is listed as a Priority Species in the Colorado and Wyoming Partners in Flight Bird Conservation Plans (Beidleman 2000, Nicholoff 2003). It is not identified as a Watch List or additional Stewardship Species in the North American Landbird Conservation Plan, where it has been assigned a combined vulnerability assessment score of 11 of a maximum of 20 (Rich et al. 2004). The Natural Heritage Program has given the white-tailed ptarmigan a global ranking of G5 and a national ranking of N5 for both the United States and Canada (available: http://www.natureserve.org/explorer). Thus, at global and national levels the species is demonstrably widespread, abundant, and secure. Within Region 2, the state ranks are S4 (apparently secure) for Colorado and S1 (critically imperiled) for Wyoming. The S1 rating for Wyoming is reflective of the species' limited distribution in this state.

White-tailed ptarmigan are legally hunted in Colorado, California, Utah, Alaska, Alberta, British Columbia (excluding Vancouver Island), Yukon Territory, and Northwest Territories. Some easily accessible ptarmigan populations may be vulnerable to over-harvest due to their unwary behavior around humans and their habit of concentrating in large flocks on traditional use areas (Braun and Rogers 1971, Braun et al. 1994a, Storch 2000).

Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

The responsibility for maintaining healthy alpine ecosystems rests largely on public land management agencies. Approximately 95 percent of the occupied habitat for white-tailed ptarmigan in Region 2 occurs on public lands, of which 84 percent is administered by the USFS (**Table 1**). Because USFS Region 2 includes the white-tailed ptarmigan on the Regional Forester's sensitive species list, by policy (USDA Forest Service 2003a), Region 2 must actively manage for ptarmigan to avoid trends towards federal listing and to maintain population viability across its range in the region. The Region must develop and implement conservation strategies for sensitive species and their habitats in coordination with other USFS units, other state and federal agencies, and private landowners. This may include collaboratively developing individual or multi-species conservation strategies, formalizing interagency conservation agreements, and incorporating recommendations into management direction set forth in Land and Resource Management Plans. The Region also must prepare Biological Evaluations on the potential effects to sensitive species of any proposed actions on lands under their administration. Scientific information from regional species evaluations, species and ecosystem assessments, and conservation strategies must be integrated into the USFS planning and implementation process. In coordination with other agencies and partners, appropriate inventories and monitoring of sensitive species must be conducted to improve knowledge of the species' distribution, status, and responses to management activities.

State and Canadian Provincial and Territorial wildlife agencies have complete management responsibilities for white-tailed ptarmigan because it is not federally listed or covered by any acts or treaties,

Table 1. Distribution of land ownership (ha) within the occupied range of white-tailed ptarmigan in USDA Forest Service Rocky Mountain Region.

Land Ownership	Colorado (%)	Wyoming (%)	TOTAL (%)
USDA Forest Service	647,550 (84)	12,998 (>99)	660,548 (84)
Private	43,380 (6)	27 (<1)	43,407 (6)
National Park Service	39,233 (5)	0	39,233 (5)
Bureau of Land Management	33,624 (4)	0	33,624 (4)
State Land Board	3,810 (<1)	0	3,810 (<1)
City/County	2,112 (<1)	0	2,112 (<1)
Non-Government Organization	243 (<1)	0	243 (<1)
U.S. Fish and Wildlife Service	181 (<1)	0	181 (<1)
TOTAL	770,133	13,025	783,158

such as the Migratory Bird Treaty Act, that may supercede the authority of the state, Canadian Province, or Territory. These agencies develop regulations, set hunting seasons, and monitor harvest. In Region 2, the white-tailed ptarmigan is classified as a game species in Colorado and Wyoming. However, due to its restricted distribution and small population size, the white-tailed ptarmigan is not hunted in Wyoming.

Ptarmigan are hunted in Colorado. The only occupied alpine areas not open to hunting in Colorado are Rocky Mountain National Park and Mt. Evans within 0.8 km (0.5 mi.) on either side of Colorado Highway 5. Although the Mt. Evans closure pertains to all hunting, it was initially established to prevent the legal shooting of mountain goats (*Oreamnus americanus*) and Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) within view of the road. Mt. Evans is easily accessible from Denver and other major metropolitan areas along the Front Range. Before the closure, harvest levels of ptarmigan on Mt. Evans exceeded 50 percent of the fall population, which significantly depressed the subsequent spring breeding population (Braun and Rogers 1971).

The hunting season in Colorado opens the second Saturday in September and closes following the first weekend in October (23 days), except in the southwestern portion of the state where the season extends into late November (72 days). Bag and possession limits are three and six, respectively. The mid-September opening date insures that young ptarmigan have attained adult size and can survive independent of the brood hen. The season closes before ptarmigan start congregating on wintering areas where they may be exceptionally vulnerable to over-harvest. The longer season in the southwest was established to allow hunters the opportunity to harvest a "white" bird. Ptarmigan occur in more remote, less accessible areas in southwestern Colorado where there is little concern about over-harvest, even after the grouse start to congregate on wintering areas.

Prior to 1998, statewide harvest estimates for white-tailed ptarmigan in Colorado were obtained from mail surveys of small game license holders. Braun et al. (1994a) considered mail surveys inadequate for estimating harvest of upland game birds because such surveys cannot be conducted in a timely fashion, response rates are low, and harvest estimates tend to be inflated due to non-response biases (i.e., successful hunters are more likely to return questionnaires). This is especially true for lesser hunted species, such as white-tailed ptarmigan. Currently, harvest estimates for Colorado are calculated using telephone surveys based on information obtained from the Harvest Information Program (HIP; available at http://www.colohip.com). This is a joint program between the Colorado Division of Wildlife and U.S. Fish and Wildlife Service, designed to improve migratory bird and small game harvest estimates. Any small game license holder who intends to hunt must validate their license by calling the HIP phone number or registering on line. At this time, they are asked a series of questions. The questioning eventually identifies those hunters who will not hunt, are somewhat likely to hunt, or are very likely to hunt white-tailed ptarmigan. Samples for the telephone survey are then selected as follows: 50 percent of those very likely to hunt ptarmigan, 20 percent of those somewhat likely to hunt, and 10 percent of those who will not hunt. The last mail survey, conducted in 1997, resulted in a harvest estimate of 2,190 ptarmigan (95 percent, CI = 845-3,535). This is more than double any estimate obtained since the initiation of the telephone survey (**Table 2**).

White-tailed ptarmigan are one of 15 upland game birds featured in the Colorado Division of

Table 2. Estimated statewide harvest of white-tailed ptarmigan in Colorado based on telephone surveys, 1998-2004.

Year	Estimated Harvest	95% Confidence Interval
1998	631	621-642
1999	418	414-422
2000	335	165-505
2001	448	258-639
2002	254	139-369
2003	975	449-1502
2004	464	306-622

Wildlife's Upland Bird Management Analysis Guide (Braun et al. 1994a). The Guide identifies and discusses 15 issues that transcend all species of upland game birds (not all issues apply to ptarmigan); it then further identifies issues specific to each species/subspecies. Three management issues specific to the white-tailed ptarmigan are listed in the Guide:

1) Some local populations may be susceptible to over-harvest because they are well known and accessible to hunters.

2) Ptarmigan use of winter habitats is precluded in some areas by human activity and development.

3) There is some demand for longer seasons so that birds in winter plumage may be harvested.

Since the Guide was completed, the Colorado Division of Wildlife has implemented regulations to address issues 1 and 3. Even before the Guide was prepared, the Colorado Division of Wildlife was concerned about the potential threats of human-related activities to ptarmigan wintering areas and took action by preparing a publication that identified 88 known accessible wintering areas for white-tailed ptarmigan throughout the state (Braun et al. 1976). This document was intended to educate land management agencies about the winter ecology and habitat requirements of white-tailed ptarmigan, and to make them aware of specific areas known to be of importance to ptarmigan during winter in hopes that these areas would be given consideration in formulating land management decisions.

The International Union for Conservation of Nature and Natural Resources and the North American Grouse Partnership have produced conservation action plans for grouse, including white-tailed ptarmigan (Storch 2000, Schroeder et al. 2004). Partners in Flight lists the white-tailed ptarmigan in conservation plans for the Southern and Central Rocky Mountains (Beidleman 2000, Casey 2000, Nicholoff 2003). The white-tailed ptarmigan also is addressed in a report to the Oregon-Washington Partners in Flight on landbird species that are not adequately monitored by the Breeding Bird Survey (Altman and Bart 2001).

Biology and Ecology

Systematics and general species description

The white-tailed ptarmigan belongs to the Order Galliformes, Family Phasianidae, and subfamily Tetraoninae. The species is believed to have been derived from ancestral rock ptarmigan stock that became isolated in the southern Rocky Mountains during the early Pleistocene (Weeden 1959, Braun 1969, Johnsgard 1973). Five subspecies have been designated. *Lagopus leucura altipetens* (southern white-tailed ptarmigan; Osgood 1901) is the subspecies found in Region 2. The other four subspecies are northern white-tailed ptarmigan (*L. l. leucurus*; Richardson in Wilson and Bonaparte 1831), Kenai white-tailed ptarmigan (*L. l. peninsularis*; Chapman 1902), Vancouver white-tailed ptarmigan (*L. l. saxatilis*; Cowan 1939), and Mt. Rainier white-tailed ptarmigan (*L. l. rainierensis*; Taylor 1920). Braun et al. (1993) questioned the validity of the subspecies designations due to the lack of comparative work. Examination of almost 1,200 museum specimens suggests that *L. l. altipetens*, *L. l. rainierensis*, and *L. l. saxatilis* are similar in size and color, and *L. l. leucurus* and *L. l. peninsularis* are closely aligned in size and color (Braun et al. 1993). No known cases of hybridization have been reported between white-tailed ptarmigan and its congeners, the rock and willow ptarmigan. However, the morphological similarities among the three species of ptarmigan may make it difficult to detect any hybrids (Weeden 1959). There also are no known cases of hybridization with blue grouse (*Dendragapus obscurus*) (Zwickel 1992), which is the only other grouse species the white-tailed ptarmigan is likely to come in contact with during the breeding season.

The genus name *Lagopus* is derived from the Latin words *lagos* and *pous*, which together mean hare-footed in reference to the dense feathers on the feet of ptarmigan that extend to the toes (Terres 1980). This feathering creates a "snowshoe" effect for walking on snow (Höhn 1977). *Leucura* originates from the Latin words leukos meaning white and oura meaning tail (Terres 1980). The white-tailed ptarmigan is the only species of grouse with completely white rectrices (tail feathers). It also is the only species of grouse found in Region 2 with white primaries. The primaries and rectrices remain white year-round.

White-tailed ptarmigan are the smallest member of the subfamily Tetraoninae. Males and females are similar in body shape and size. Two age classes can be identified throughout the year based on the presence (subadult) or absence (adult) of black pigmentation on the two outer primaries and the outer primary covert (Braun and Rogers 1967, Braun and Rogers 1971). Adults measure 30 to 34 cm in length. Body mass averages 345 to 410 g for males and 350 to 425 g for females depending on time of year and age class (May 1975, Braun et al. 1993). White-tailed ptarmigan have 10 primaries, 16 rectrices, and 16 secondaries (Braun et al. 1993). They are in an almost continual state of molt from April to November and are completely white during winter except for their black eyes, toe nails, and beak (Braun et al. 1993). During the breeding season, males have a conspicuous hood and necklace of coarsely-barred brown and black feathers (Johnsgard 1973, Braun et al. 1993). Females are mottled brown and black with yellow barring (absent in males) on their head, breast, flanks, back, and upper tail coverts (Johnsgard 1973, Braun et al. 1993). Males retain pure white lower breast, abdomen, and under-tail coverts throughout the year, whereas females replace these feathers with more subdued yellowish-brown or buff colored feathers with black barring (Braun et al. 1993). Both genders have eyecombs, but the combs are more prominent and vividly red on males compared to females (Braun et al. 1993). Males and females in summer plumage appear gray to light gray-brown as the barred feathers indicative of the breeding plumage are replaced by finely vermiculated, speckled gray and reddish-brown colored feathers on the dorsal surface and flanks (Braun and Rogers 1971). Females retain some of the black, brown, and yellow-barred feathers characteristic of their breeding plumage primarily on the nape, flanks, and inner wing (Braun and Rogers 1971). The undersides remain the same, white on males and yellow-brown to buff with barring on females.

Distribution and abundance

White-tailed ptarmigan are endemic to alpine habitats in the high cordillera of western North America (**Figure 2**; Aldrich 1963, Braun et al. 1993). This unique alpine grouse is one of just five avian species that regularly completes its breeding and nesting activities in alpine habitats above treeline (Braun 1980). In addition, it is the only species of ptarmigan that is not circumpolar in distribution (Aldrich 1963). In the northern portion of its range, the white-tailed ptarmigan occurs sympatrically with willow and rock ptarmigan. South of central British Columbia, the white-tailed ptarmigan occurs allopatrically in relation to the other ptarmigan species. White-tailed ptarmigan range as far north as south-central Alaska, north-central Yukon Territory, and extreme western portions of the Northwest Territories. From here the distribution extends southward along the Coast Mountains of British Columbia into the Cascade Mountains of Washington to Mount Rainier, and south along the Rocky Mountains through southwestern Alberta to northern New Mexico (Aldrich 1963, Clarke and Johnson 1990). Populations also occur on Vancouver Island, British Columbia (Martin et al. 2004). The alpine habitats of white-tailed ptarmigan have remained relatively unexploited. Thus, the species still occupies most of its historical range (Braun et al. 1993) although it may be extirpated from some historically occupied areas in New Mexico (Ligon 1961).

The distribution of white-tailed ptarmigan is not continuous, nor are all seemingly suitable habitats occupied (Aldrich 1963, Braun and Pattie 1969, Scott 1982, Braun 1988, McEneaney 1995, Wright 1996). No valid records exist for white-tailed ptarmigan in Idaho, Oregon, California, or Utah (Aldrich 1963, Braun et al. 1978, Clarke and Johnson 1990, Braun 1993, Braun et al. 1993). In addition, there are no published accounts of white-tailed ptarmigan in the Olympic Mountains in northwestern Washington. The absence of ptarmigan in California, Oregon, Utah, and Olympic Mountains has been attributed to the isolation of suitable alpine habitats from the nearest occupied ranges. The absence of ptarmigan in Idaho is due to the lack of suitable alpine habitats. Published reports of ptarmigan occurring in Idaho, Oregon, and Utah (Gabrielson and Jewett 1940, Rush 1942, Twomey 1942, Arvey 1947, Woodbury et al. 1949) are not based on valid evidence such as photographs or specimens. The reports are most likely sightings of blue grouse, which frequently venture above treeline during summer where they are commonly mistaken for ptarmigan.

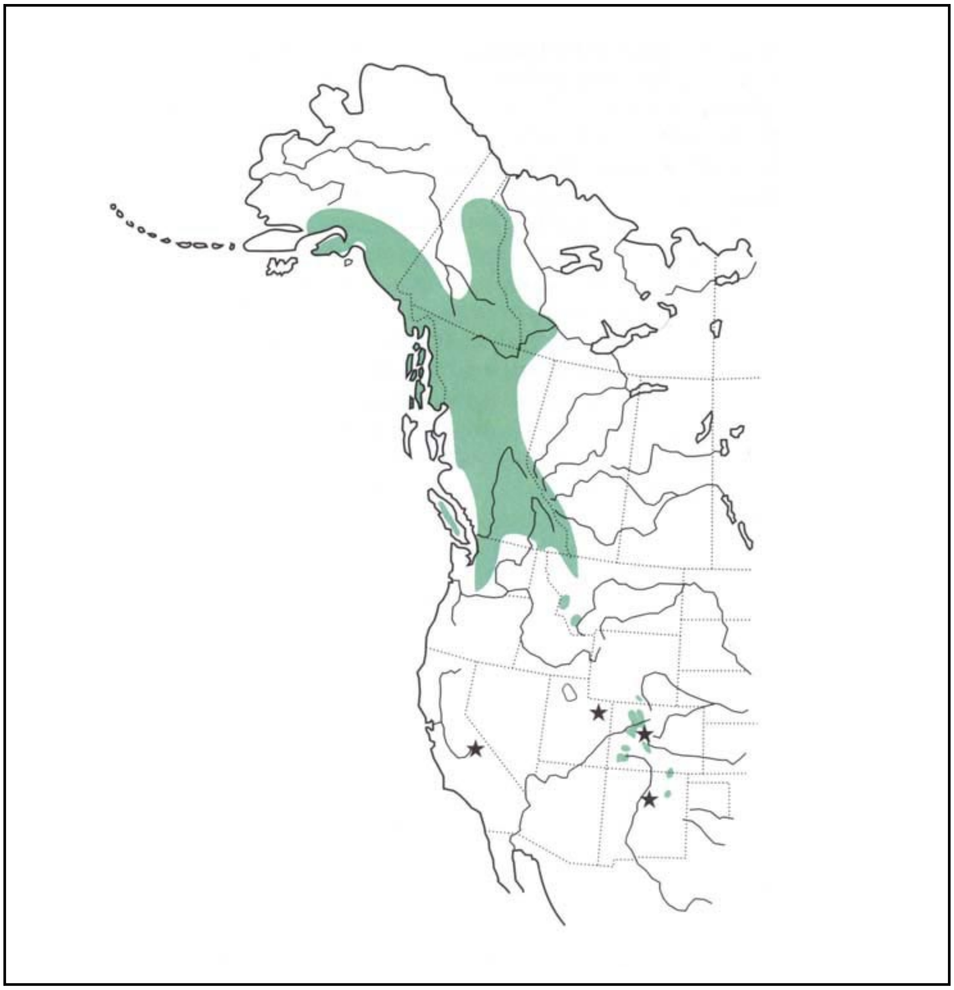

Figure 2. Known distribution of white-tailed ptarmigan. Stars show locations of successfully introduced populations.

Weeden (1959) postulated that white-tailed ptarmigan are quite recent north of the international boundary between the United States and Canada, and they may eventually pioneer further north into the Kuskokwim Mountains, Brooks Range, and the entire Mackenzie Mountain system. In addition to the possibility of natural expansion, the species also has been successfully introduced into suitable habitats outside its native range, including the Sierra Nevada in California (Clarke 1989, Clarke and Johnson 1990, Frederick and Gutierrez 1992), Uinta Mountains in Utah (Braun et al. 1978), and the Pecos Wilderness Area in New Mexico (Hubbard and Eley 1985). White-tailed ptarmigan also were released into the Wallowa Mountains in northeastern Oregon, but the translocation was unsuccessful (Evanich 1980, Braun 1993).

Within Region 2, white-tailed ptarmigan only occur in Colorado and Wyoming (**Figure 3**). The species occurs in the following 11 national forests in Region 2: Arapaho, Roosevelt, Uncompahgre, Gunnison, Medicine Bow, Routt, Pike, San Isabel, Rio Grande, San Juan, and White River (**Table 3**). Whereas the distribution of this alpine grouse is clearly documented in Colorado (Braun and Rogers 1971), its distribution in Wyoming is uncertain (McCreary 1939, Braun and Pattie 1969, Braun 1988, McEneaney 1995).

Wyoming has about 340,362 ha of alpine habitat scattered from the southeastern to the northwestern portion of the state. Clarke and Johnson (1990) omitted Wyoming from their white-tailed ptarmigan range map because they claimed the reports of ptarmigan in Wyoming were anecdotal and unverified. However, Harju (1977) and Braun (1988) presented valid evidence of white-tailed ptarmigan in the Snowy Range in southeastern Wyoming. Gates (1940) also reported the presence of ptarmigan in this area. McCreary (1939) reported that white-tailed ptarmigan were present in the Wind River Mountains, on Cloud Peak in the Bighorn

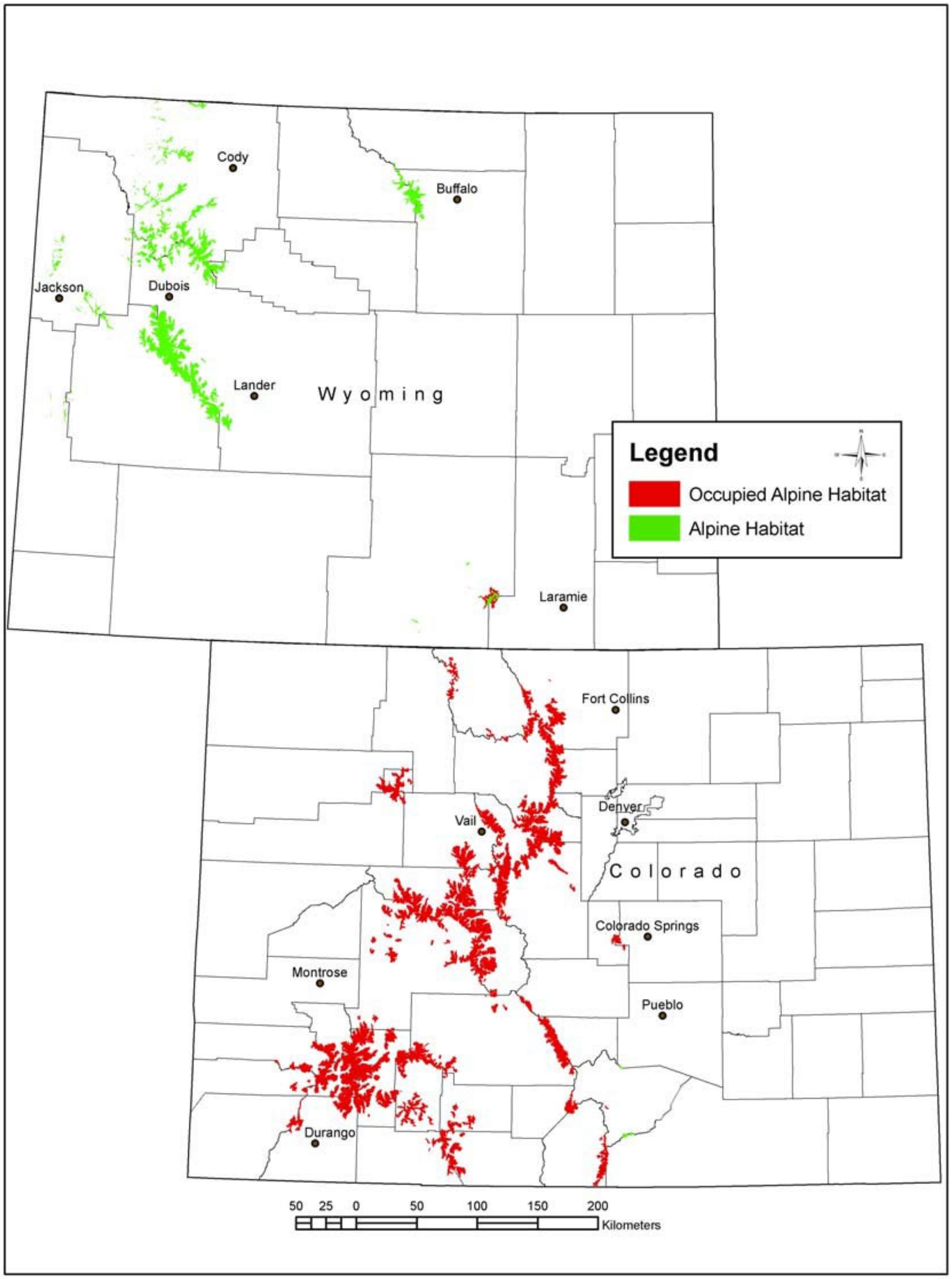

Figure 3. Distribution of white-tailed ptarmigan within the Rocky Mountain Region (Region 2) of the USDA Forest Service.

Table 3. Distribution of alpine habitats occupied by white-tailed ptarmigan in USDA Forest Service Rocky Mountain Region.

National Forest	Area (ha) of Occupied Range
Pike-San Isabel	138,522
White River	133,129
Grand Mesa-Uncompahgre-Gunnison	107,067
Rio Grande	105,540
San Juan	80,040
Arapaho-Roosevelt	68,581
Routt-Medicine Bow	27,669
TOTAL	660,548

Mountains, on Quadrant Mountain in Yellowstone National Park (apparently based on Skinner's [1927] report), and in the Snowy Range, but he provided no valid evidence to support his findings. Rosche (1954) reported observing one ptarmigan up close above treeline on the southeast side of Mt. Washburn in Yellowstone National Park on 20 July 1952. Pattie and Verbeek (1966) failed to find ptarmigan in the Beartooth Mountains. Braun (1988) searched alpine habitats for ptarmigan in Wyoming during 1966-67 (Snowy Range), 1968 (Beartooth Plateau), 1977 (Bighorn Mountains), and 1987 (Wind River Mountains), but only found ptarmigan or ptarmigan sign in the Snowy Range. Braun (1988) further reported that alpine habitats in the Wind River and Bighorn mountains appeared to be suitable for white-tailed ptarmigan, but alpine habitats on the Beartooth Plateau were marginal due to the lack of breeding and winter use sites. Most recently, McEneaney (1995) found no evidence of white-tailed ptarmigan in Yellowstone National Park and recommended that all field guides and scientific publications should refrain from listing Yellowstone as definitive habitat for white-tailed ptarmigan until conclusive evidence is obtained.

Based on these reports, white-tailed ptarmigan appear to be absent from most alpine habitats in Wyoming, except possibly for the Snowy Range. The biological evaluation of white-tailed ptarmigan presented in Appendix I of the Revised Land and Resource Management Plan for the Medicine Bow National Forest (USDA Forest Service 2003b) lists the species as present in the Snowy Range historically, but currently considers them to be extirpated from the Snowy Range. Although there have been anecdotal reports that ptarmigan persist in the Snowy Range, there have been no confirmed sightings since the early 1970s (Harju 1977). The area is heavily used for recreation during all seasons of the year and is a favorite spot visited by birdwatchers looking specifically for alpine species. It is unlikely that there would be no observations of ptarmigan in over 30 years if the birds persisted in the Snowy Range.

Suitable habitat for white-tailed ptarmigan in the Snowy Range is limited. Until 1997, the area was subjected to intensive grazing by domestic sheep. Currently the area receives high recreational use, including unlimited snowmobile access in winter. The combination of these factors may have contributed to the demise of this small, isolated population. Immigration from the nearest occupied habitats in Colorado (i.e., Mt. Zirkel Wilderness Area or Crown Point Mountain) may still occur, but in insufficient numbers to recolonize the area. It also is possible that habitat has been degraded to the point that it can no longer support a self-sustaining population of ptarmigan.

Colorado supports the most extensive distribution of white-tailed ptarmigan in the United States outside of Alaska. There are an estimated 3,370,000 ha of alpine in the western United States south of Canada (USDA Forest Service 1972); approximately one-fourth (770,133 ha) of this is in Colorado. Braun and Rogers (1971) estimated that the occupied range of white-tailed ptarmigan in Colorado encompassed 9,712 km^2. Their estimate included some areas below treeline. They concluded this grouse inhabits nearly all alpine areas in the state. The only areas above treeline in Colorado where ptarmigan did not naturally occur are the Spanish Peaks, Greenhorn Mountain, and Pikes Peak. The absence of ptarmigan on the Spanish Peaks can be attributed to the almost complete deficit of vegetation above treeline. Suitable habitat occurs on Greenhorn Mountain but is insufficient (<2 km^2) to maintain a population. Pikes Peak contains adequate (>23 km^2) and suitable habitat, but due to its insular nature from the nearest occupied range (60+ km), it did not support a population of white-tailed ptarmigan until the species was successfully introduced there in 1975 (Hoffman and Giesen 1983).

While the distribution of white-tailed ptarmigan appears to be unchanged from historic levels, population sizes and trends are mostly unknown other than in localized areas of study. The exceptions are in areas where translocation efforts have expanded the range (Braun et al. 1993) and at the southern periphery of the species' range in New Mexico where the distribution has retracted slightly northward due to habitat degradation (Ligon 1961). Storch (2000) reported a crude, range-wide, spring population estimate of more than 200,000 birds. The North American Landbird Conservation Plan lists the global population of white-tailed ptarmigan at 2,000,000 (Rich et al. 2004); this appears to be an extremely inflated estimate and may be a reporting error.

Breeding densities fluctuate widely between years and locations and range from two to 14 birds per km^2 (Choate 1963, Braun and Rogers 1971, May 1975, Hoffman and Giesen 1983, Clarke and Johnson 1992, Frederick and Gutierrez 1992, Martin et al. 2000). Within Region 2, breeding densities have been estimated for several locations in Colorado using play-back of tape-recorded male challenge calls to locate territorial males (**Table 4**; Braun et al. 1973). Assuming an average breeding density of 6 birds per km^2 and 9,712 km^2 of occupied habitat (Braun and Rogers 1971), the breeding population of ptarmigan in Colorado approximates 58,270 birds. However, probably no more than 60 percent of the alpine areas delineated by Braun and Rogers (1971) as occupied by ptarmigan constitutes suitable breeding habitat, the remainder being winter and summer habitat. Thus, a more realistic estimate of the breeding population of ptarmigan in Colorado based on approximately 5,800 km^2 of suitable breeding habitat is 34,800 birds. No density estimates are available for Wyoming. Currently, ptarmigan may be extirpated from the only known occupied habitat in Wyoming, the Snowy Range (USDA Forest Service 2003b). In the past, the total population was likely small due to the poor quality and limited amount of available habitat.

Activity patterns and movements

Winter season

White-tailed ptarmigan are gregarious and generally associate in flocks, except during the breeding and nesting seasons from late April to early July (Braun et al. 1993). Flocking tendencies are most evident from late October until mid-April when birds are concentrated on winter use sites (Braun et al. 1976, Hoffman and Braun 1977, Giesen and Braun 1992). Of 185 ptarmigan encounters during winter reported by Braun et al. (1976), only 7 percent were of lone birds and 69 percent were of flocks containing two to 25 individuals; average flock size was 15.5 and ranged from two to 97 birds. Bergerud (1988) postulated that flocking of grouse in winter is advantageous for sharing or obtaining information on food distribution and for predator detection, both of which may increase survival of individual flock members.

Partial segregation by gender occurs on winter use sites (Braun and Schmidt 1971, Hoffman and Braun 1977). Males, especially adults, tend to winter at slightly higher elevations than females (Braun and Schmidt 1971, Braun et al. 1976, Hoffman and Braun

Table 4. Estimated breeding densities (birds/km^2) of white-tailed ptarmigan at study sites throughout Colorado.

Location	Mean Density (Range)	Years	Source
Mt. Evans	6.3 (2.2-10.3)	1966-91	Braun and Giesen 1992
Rocky Mountain National Park	8.6 (4.5-13.5)	1966-91	Braun and Giesen 1992
Niwot Ridge	8.3 (6.4-9.5)	1970-74	May 1975
Crown Point	6.6 (5.6-8.2)	1966-69	Braun and Rogers 1971
Mesa Seco	5.7 (5.3-6.2)	1966-67, 69	Braun and Rogers 1971
Independence Pass	7.4 (6.9-8.3)	1966-69	Braun and Rogers 1971
Square Tops	3.5 (2.7-4.4)	1993-96	Martin et al. 2000
Guanella Pass	5.0 (2.1-6.4)	1990-96	Martin et al. 2000
Loveland Pass	4.7 (4.4-4.8)	1990-92	Martin et al. 2000
Pikes Peak[1]	6.0 (3.4-8.4)	1976-80	Hoffman and Giesen 1983

[1] Introduced population

1977). Adult males also tend to associate in smaller flocks during winter than females (Hoffman and Braun 1977). This spatial and habitat segregation may reflect a strategy of males to winter closer to their breeding territories to give them a competitive advantage in securing breeding space. It also reduces competition with females for limited winter resources. Subadult males are more likely to associate with females during winter than adult males (Braun et al. 1976). Braun et al. (1976) found no evidence that winter flocks were composed of family units or the same individuals associated together throughout the winter. They documented considerable interchange of members among flocks and noted that smaller flocks would frequently join to form larger flocks, then disassociate into smaller flocks again that were not necessarily composed of the same individuals.

During the day, ptarmigan remain sedentary, sitting quietly in shallow snow burrows (Braun and Schmidt 1971). On windy days, they make seek shelter behind rocks or within krummholz areas alternately dominated by clumps of low-growing Engelmann spruce (*Picea engelmannii*) and willow (*Salix* spp.). If conditions are extremely cold and windy, they may roost beneath the surface of the snow or move to treeline. Intensive feeding bouts take place in the early morning and late evening hours with less intensive feeding occurring periodically during the day (Braun and Schmidt 1971). When feeding during the day, ptarmigan move slowly and cautiously. They may remain stationary and peck at a single willow bush for several minutes before moving to the next bush. The level of activity is heightened during the morning feeding interval and increases even more during the evening feeding period, to the point where feeding appears almost frenzied as the birds run and sometimes fly from one willow bush to another. Individual birds will jump or stretch as far as they can to reach buds overhead or fly into the bush and attempt to balance themselves on the narrow, flimsy branches while trying to peck willow buds. During mid-winter, over 12 hours may lapse between the evening and morning feeding periods. Thus, the intense evening feeding behavior of ptarmigan is most likely an effort to fill their crops to capacity before going to roost.

Just before dark, the birds stop feeding almost simultaneously, and after a brief period of inactivity, the entire flock takes flight to another location where they roost for the night (Braun and Schmidt 1971). In the morning, the birds may feed for a short period in the immediate vicinity of where they roosted overnight, but they usually fly to another site to feed and spend the day.

Ptarmigan roost beneath the surface of the snow at night (Braun and Schmidt 1971). This is one of several behavioral and physiological adaptations of ptarmigan for staying warm and conserving energy during the winter (Martin et al. 1993). Areas used for night roosts tend to be in sheltered locations with over 300 mm of soft snow (Braun and Schmidt 1971). The average depth of a night roost is 160 mm (range = 90-270 mm, *n* = 80) with about 30 to 50 mm of snow covering the submerged bird (Braun and Schmidt 1971). Ptarmigan do not "plunge" into the snow to roost like ruffed grouse (*Bonasa umbellus*; Runkles and Thompson 1989). Instead, they dig, push, and wiggle their way into the burrow often tunneling under the snow for 150 to 600 mm (Braun and Schmidt 1971). Occasionally they stick their head above the snow surface, especially if they are roosting beneath the snow during the day.

Ptarmigan of both genders show a high fidelity to wintering areas similar to their attachment to breeding sites (Braun et al. 1976, Hoffman and Braun 1977, Giesen and Braun 1992). Studies have indicated about 60 percent of the birds return to the same wintering area (Hoffman and Braun 1977). Adults exhibit a greater affinity for wintering areas than subadults (Braun et al. 1976). One factor attributing to this difference is that subadults have higher mortality rates than adults (Braun 1969, May 1975); therefore, fewer live long enough to return. However, Braun et al. (1976) also suggested that some subadults may disperse from wintering areas where they were initially banded and subsequently winter elsewhere. This is certainly the case for subadult males that are successful in establishing a territory in their first spring. If suitable winter habitat occurs closer to their territory than where they wintered the previous year, they will use the closest habitat and not return to the area used the previous winter.

Daily movements on wintering areas vary depending on snow conditions. Giesen and Braun (1992) reported an average winter home range (minimum convex polygon; Mohr 1947) of 1.50 km^2 ± 0.77 SD for 17 females (1.62 km^2 ± 0.72 SD) and two males (0.44 km^2 ± 0.20 SD). When ptarmigan first arrive on wintering areas, food is abundant and snow depths are minimal. Because temperatures are cold but not severe at this time, the need to snow roost at night is not as critical. Daily movements at this time may be less than 200 to 300 m. With increasing snow fall, food availability decreases and daily movements increase. Braun and Schmidt (1971) observed one flock that moved over 1,500 m over the course of a single day while feeding. They described the movements as circular, with much of the same area covered during the day. Movements also increase as weather conditions become more severe. The birds may feed on exposed ridges and then fly to more sheltered areas near treeline to loaf during the day. They may fly back to the exposed sites to feed in the evening and then fly to an area with soft snow to roost for the night.

Martin et al. (2000) found a lack of movements to wintering sites during the mild winter of 1997-98. Most of their radio-marked birds did not leave the breeding range to winter elsewhere. They suggested that white-tailed ptarmigan may not migrate or may migrate shorter distances during mild winters when food supplies are more widely distributed at higher elevations.

Breeding season

Ptarmigan generally move from low elevation wintering areas to mid-elevation breeding areas (Braun et al. 1993). Departure from wintering areas and subsequent territory formation can begin in early April, but birds may return to winter use sites in the event of prolonged severe weather (**Table 5**). Most males are on territories by late April (**Table 5**), which is when females begin to arrive (Braun 1984, Schmidt 1988). Females move through breeding areas either singly or in small flocks.

Females move greater distances between wintering and breeding areas than males (Braun and Schmidt 1971, Hoffman and Braun 1975, Herzog 1980). Using data presented by Hoffman and Braun (1975), Braun et al. (1993) reported the following average distances moved between wintering and breeding areas: females = 7.3 km ± 5.3 SD, range = 1.3-22.7 km, *n* = 67; males = 3.2 km ± 2.6 SD, range = 0.2-10.8 km, *n* = 32. These estimates are based on ptarmigan banded on wintering areas and relocated on breeding areas. The effort required to relocate marked birds was limited by the vastness and remoteness of the areas that needed to be searched. Thus, maximum distances moved to breeding areas were likely underestimated. Braun et al. (1993) reported that two males transplanted in spring to another breeding site traveled 43 and 50 km across primarily forested landscapes to return to their original territories. This information suggests that white-tailed ptarmigan are capable of moving long distances across atypical habitats.

Territory size varies temporally and with location. Temporal variation is caused by changing snow conditions as the breeding season progresses. Territory size expands uphill as snow melts and more food and cover are exposed (Schmidt 1988, Braun et al. 1993). Variation due to location is related to habitat quality and, in some areas, hunting pressure. In better habitats, requisite resources can be obtained within a smaller area, thus, territories are smaller. However, excessive hunting pressure can reduce densities (Braun and Rogers 1971, Braun et al. 1993). With fewer males returning to breed, territories of surviving males may become larger.

The size of 28 breeding territories on Mt. Evans ranged from 4.9 to 67.1 ha and averaged 28.1 ha ± 18.9 SD (Braun et al. 1993). White-tailed ptarmigan in Rocky Mountain National Park defended territories ranging in size from 6.5 to 9.3 ha (mean = 7.8 ha ± 1.0 SD, *n* = 5) in 1967 and 9.3 to 19.0 ha (mean = 14.4 ha ± 2.8 SD, *n* = 7) in 1968 (Schmidt 1988). Schmidt (1988) considered the

Table 5. Approximate timing of seasonal movements and breeding, nesting, brood-rearing, and winter activities of white-tailed ptarmigan in USDA Forest Service Rocky Mountain Region.

Activity	**Approximate Timing (Peak)**
Movements to breeding areas	Mid-April-early May (late April)
Pair formation	Mid April-mid-May (late April-early May)
Breeding season	Mid-April-early July (late April-late June)
Nesting season[1]	Early June-early August (mid-June-mid-July)
Egg laying[1]	Early June-mid-July (mid-June)
Incubation[1]	Mid-June-mid-July (late June-early July)
Hatching	Late June-early August (early-mid-July)
Brood-rearing season	Late June-late-September (mid-July-mid-September)
Movements to summer areas	Late June-mid-July (early-mid-July)
Movements to winter areas	Late October-mid-November (early November)
Winter season	Late October-late April (mid-November-early April)

[1] Includes renesting activities.

1968 data more accurate because it was based on more observations of territorial activity. Schmidt (1988) also acknowledged the territorial boundaries he delineated represented the outer most limits that males visited when challenging other territorial males. He reported that most of the time (>80 percent of all observations), territorial males and their mates were observed within much smaller areas referred to as "maximum use" areas. Maximum use areas averaged 2.1 ha ± 0.6 SD and 3.9 ha ± 1.4 SD in 1967 and 1968, respectively.

Vigorous defense of territories by males coincides with the arrival of females (Schmidt 1969, 1988). Principle displays associated with territorial defense and maintenance include male flight screams, ground challenges, and female flight screams (Schmidt 1969, 1988). Courting displays include calling, wing dragging, tail-fanning, and head bobbing (Schmidt 1969, 1988; Braun et al. 1993). Pair formation, especially for previously mated pairs, is established within a few days after the females arrive and usually remains stable throughout the duration of the breeding season (Hannon and Martin 1996). If both members of the pair return, they generally occupy the same territory in consecutive years (Braun and Rogers 1971, Schmidt 1988, Hannon and Martin 1996). However, some females may remain with a particular mate for several weeks before moving to another territory of a different male to nest; or if they lose their first clutch they may move to the territory of another male to renest (Hannon and Martin 1996). Ptarmigan tend to select mates of the same age class (Hannon and Martin 1996). Braun et al. (1993) presented data on 121 pairs consisting of the following age combinations: 53 (44 percent) adult male-adult female, 21 (17 percent) subadult male-subadult female, 43 (36 percent) adult male-subadult female, and four (3 percent) subadult male-adult female.

Monogamy is the predominant breeding strategy for white-tailed ptarmigan (Wittenberger 1978); polygamy is uncommon, and polyandry is virtually nonexistent (Braun and Rogers 1971, Schmidt 1988, Braun et al. 1993, Hannon and Martin 1996). Of 293 territorial males monitored by Hannon and Martin (1996), 93 percent were monogamous and 7 percent were polygamous. Benson (2002) found white-tailed ptarmigan in Glacier National Park to be nearly genetically monogamous; of 58 chicks with putative fathers identified, only 3 percent were the result of extra-pair copulations. In addition, only three of 18 (17 percent) clutches contained extra-pair offspring.

Hannon and Martin (1996) found that mate fidelity is the norm as only 14 to 20 percent of the pairs change mates from one breeding season to the next, provided both members of the pair survive. Even so, pair durations are short, lasting on average less than two years primarily because of high annual mortality in both sexes (Hannon and Martin 1996). If the female dies, the male tends to remain on the same territory and takes another mate. If the male dies, the female may remain on the territory and bond with the male that takes over the territory, or more likely she selects another mate on a different territory. Hannon and Martin (1996) documented that 21 percent of white-tailed ptarmigan females switched mates to renest after their first clutch was depredated. In most cases, whether the separation takes place within or between seasons, it appears that females are the ones to initiate the "divorce" since they move to another territory while their previous mate stays on the former territory (Hannon and Martin 1996).

Within the breeding season, the pair bond can last from 2.5 to 3 months (**Table 5**). During this time, the individuals of a pair remain in close proximity (0.5 to 20 m). The male may leave for short periods to defend his territory against neighboring territorial males or intruding non-territorial males. Otherwise, the male accompanies the female almost continuously (88 to 92 percent of sightings) from pair formation until incubation, and while accompanying his mate, he spends 22 to 30 percent of his time displaying vigilant behavior (Artiss and Martin 1995). This behavior primarily functions to maximize the rate of energetic gain of females during the pre-incubation period by allowing them to spend more time foraging and less time watching for predators (Artiss and Martin 1995, Artiss et al. 1999).

Sex ratios vary from 0.8 to 1.9 males per female but most commonly tend to be skewed in favor of males due to higher mortality of females (Braun et al. 1993). Consequently, up to 26 percent of males may remain unmated in some years, whereas unmated females, including subadults, are extremely rare (Schmidt 1988, Hannon and Martin 1996). Males often have more mates in a lifetime than females because males live longer and because some males are polygynous (Hannon and Martin 1996). Adult males return to the same territory occupied the previous year (Schmidt 1969, 1988). Subadult males frequently occupy marginal territories that seldom attract females; therefore, they may move to a different, higher quality territory their second year (first year as an adult). Exceptions occur on heavily hunted areas where subadult males are more successful in acquiring quality territories and attracting a mate (Braun 1969, 1984; Braun and Rogers 1971).

Nesting season

Timing of white-tailed ptarmigan nesting events is directly controlled by photoperiod, but it may be accelerated or delayed annually by climatic conditions (Braun and Rogers 1971, Giesen et al. 1980). Females do not begin nesting activities until they are completely in alternate (nuptial) plumage (Braun and Rogers 1971). Although ultimately controlled by day length (Host 1942), initiation and progression of the pre-alternate molt is further controlled by amount of snow cover and resulting light intensity (Braun and Rogers 1971, Giesen et al. 1980). Thus, during years with early snow melt or prolonged snow cover, nesting activities can be accelerated or delayed 1 to 2 weeks, respectively.

Nest construction and initiation of egg laying begin in early to mid-June, with incubation starting in mid- to late June, and hatching occurring in early to mid-July (**Table 5**; Giesen and Braun 1979b, Giesen et al. 1980, Braun et al. 1993, Wiebe and Martin 1998a). Mean date for initiation of laying of 143 first clutches at Mt. Evans, Colorado was 8 June ± 5.5 (SD) days and ranged from 25 May to 20 June; initiation of 65 renest clutches ranged from 12 June to 11 July with a mean initiation date of 26 June ± 7.0 (SD) days (Braun et al. 1993). Incubation usually commences with laying of the last egg, but some females start incubation the day after the last egg is laid (Braun et al. 1993). Giesen et al. (1980) reported the incubation period as 22 to 23 days, whereas Martin et al. (1993) and Braun et al. (1993) both report the incubation period as 25 days (range 24-26 days). Mean date of hatch for 42 first clutches and 25 renest clutches at Mt. Evans was 7 July ± 5.1 (SD) days (range = 24 June to 16 July) and 25 July ± 6.4 (SD) days (range = 12 July to 4 August), respectively (Braun et al. 1993). The 12-year median hatch date (includes renests) reported by Giesen et al. (1980) for white-tailed ptarmigan in Rocky Mountain National Park was 15 July and varied from 6 July to 23 July.

Construction of the nest, incubation of the eggs, and care of the young are activities performed exclusively by the female. The nest is a shallow, bowl-shaped depression on the ground lined with dried vegetation and several soft body feathers (Giesen et al. 1980). The average inside dimensions of the nest bowl are 151 mm in length, 130 mm in width, and 36 mm deep (Giesen et al. 1980). The female may construct several nest scrapes before selecting one in which to lay her clutch. She will lay eggs anytime during daylight hours (0700-2000 hours), but the peak laying period occurs during mid-day between 1000 and 1300 hours (Giesen et al. 1980, Wiebe and Martin 1995). There is no evidence to suggest that egg deposition occurs after dark.

The hen may remain on the nest for several hours after an egg is deposited, especially as the clutch nears completion, but incubation does not begin until the last egg is deposited (Giesen et al. 1980). Females lay on average 0.8 eggs per day ± 0.2 SD (Martin et al. 1993, Wiebe and Martin 1995). Giesen et al. (1980) reported intervals between successive eggs of 26 to 30 hours. Wiebe and Martin (1995) found the laying interval to be bimodal, with 67 percent of females laying successive eggs between 24 and 30 hours (mean = 26.3 hours) apart and the remaining 33 percent laying successive eggs at 40 to 47.5 hour (mean = 43.7 hours) intervals. Severe spring snow storms may cause some delays in laying. Laying rates vary considerably between individuals from 0.4 to 1.0 eggs per day (Wiebe and Martin 1995). If an egg is laid late in the day (after 1500 hours), there is a high probability that the female will skip laying the following day and not lay the next egg until 40+ hours after the previous egg was laid (Wiebe and Martin 1995). Before leaving the nest the female gathers pieces of vegetation and completely covers the eggs (Giesen and Braun 1979b). Sometimes the male will accompany the female to the nest during the construction and laying period, but most often he stands guard nearby. The male does not visit the nest once the female starts incubation.

Eggs are oval in shape and contain moderate to heavy reddish-brown or chestnut colored blotches or speckles on a creamy brown to light cinnamon background (Giesen et al. 1980, Braun et al. 1993). The color fades as the incubation period progresses. Eggs average 43.7 mm ± 1.7 SD (range = 39.2-48.9 mm) in length and 29.7 mm ± 0.7 SD (range = 27.2-31.4 mm) in breadth (Giesen et al. 1980, Braun et al. 1993).

All females attempt to initiate at least one clutch (Braun et al. 1993). Females are extremely attentive (incubation constancy = 95 percent) and protective of the nest and are reluctant to leave when disturbed (Giesen and Braun 1979b). They will retrieve eggs that are displaced less than 18 cm from the nest (Giesen 1978). This behavior insures the continued incubation of the egg and, more importantly, increases the survival of the hen and the rest of the clutch as eggs outside the nest may attract ground or avian predators (Giesen 1978).

Incubating females almost invariably take recesses at dawn and dusk, and sometimes they take one or more daytime recesses (Giesen and Braun 1979b;

Wiebe and Martin 1997, 2000). Daytime recesses are of shorter duration than crepuscular recesses, with the longest recesses taken at dusk. While crepuscular recesses occur within narrow time limits, timing of daytime recesses is much more variable. Wiebe and Martin (1997) reported the following approximate start times and length of the recesses: dawn recess starts at 0500 hours and lasts 25 minutes, day recess starts at 1300 hours and lasts 20 minutes, and dusk recess starts at 2000 hours and lasts 31 minutes.

During the incubation recess, the hen flies 50 to 800 m to a feeding site where she is immediately joined by the male (Giesen and Braun 1979b, Wiebe and Martin 1997). She may use the same feeding site on successive recesses, but more often she uses a different site. The male stays within 5 m of the hen, remains vigilant at all times, and does not feed. The female feeds voraciously during the majority of the incubation break and pays little attention to the male. She spends a small amount of time preening, dust bathing, and walking around before flying back to the nest. She lands within a few meters of the nest and immediately walks the remaining distance and settles on the nest. Timing of recesses appears to be related to microclimate at the nest and body condition of the female (Wiebe and Martin 1997), rather than a strategy to avoid predators (Giesen and Braun 1979b, Angelstam 1984, Erikstad 1986).

Older females tend to initiate laying earlier, lay larger clutches, and renest at higher rates than younger birds (Giesen and Braun 1979c, Giesen et al. 1980, Braun et al. 1993, Wiebe and Martin 1998a, Sandercock et al. 2005a). Clutch size for initial nests varies from four to eight eggs (Giesen et al. 1980, Braun et al. 1993). Average clutch size of females at least 2 years old (6.2 eggs ± 0.7 SD) is larger than for females less than 2 years old (5.8 eggs ± 0.9 SD). Older females also start laying eggs on average 2 days earlier than younger females (Wiebe and Martin 1998a). Renest clutches are only produced if the first clutch is destroyed or abandoned. White-tailed ptarmigan rarely attempt to renest more than once (Braun et al. 1993). Renest clutches are smaller than first clutches, ranging from two to six eggs per clutch (Braun et al. 1993). Renest clutches are only slightly larger for females at least 2 years old (4.8 eggs ± 0.7 SD) than those less than 2 years old (4.6 eggs ± 0.9 SD). However, the renesting rate (percent of hens that renest after losing their first clutch) is higher for females at least 2 years old (80 percent) than for females less than 2 years old (45 percent) (Wiebe and Martin 1998a, Sandercock et al. 2005a).

Summer/brood-rearing season

Males abandon territories during the late stages of incubation (**Table 5**), move upslope to rocky areas near late-lying snowfields, and gather into flocks (Braun 1969, Schmidt 1988). Likewise, females that fail to successfully hatch a clutch of eggs abandon their territories, move upslope, and join flocks of males. The flocks usually consist of 10 to 15 birds, but they can vary from two to over 30 birds. Movements from breeding to summering areas seldom exceed 1.5 km although movements over 22 km have been documented (Braun 1969). In some cases, depending on the juxtaposition of breeding and summering areas, birds may need to move laterally for several kilometers before moving upslope. This is the situation on Mt. Evans, Colorado. Breeding territories are located on ridges that extend for several kilometers from the higher slopes of Mt. Evans where the birds summer. Here, movements to summering areas tend to be 2 to 3 km further than movements documented elsewhere in Colorado (Braun 1969).

Once males and unsuccessful females reach suitable summer habitat, their movements become localized, and they usually remain within the same general area throughout the summer, typically occupying an area less than 50 ha (Braun 1969, Schmidt 1988). Occasionally, some birds may move 2 to 3 km between several summer use areas (Schmidt 1988). However, traditionally, ptarmigan tend to use the same summer areas year after year. Summering areas used during years of normal and above average precipitation may be abandoned during dry years in favor of areas with better moisture. Such areas may be located downhill from traditional summer use areas.

Females and their young abandon the nest site soon after the last egg hatches. Movements following hatch may vary from one year to the next depending on moisture conditions. Movements also may vary within years among broods and between different areas. During the first few days following hatch, most broods remain within a few hundred meters of the nest (Giesen 1977, Schmidt 1988). Documented movements between breeding and brood-rearing areas range from 0 to 3,300 m, averaging less than 1,000 m (Braun 1969, Giesen 1977, Schmidt 1988). Some hens raise their broods on or near their breeding territory while others gradually move upslope to brood-rearing areas. Brood ranges, like territories, are used consistently from year to year. Brood ranges are usually located at slightly lower elevations than summering areas used by males and unsuccessful females. It is not uncommon for eight to ten broods to concentrate in an area less than 100 ha. Brood home ranges calculated for nine broods in Rocky Mountain National Park ranged from 3 to 32 ha and averaged 15.4 ha (Giesen 1977). Daily movement patterns within the home range were circular or elliptical in shape, with the same route often traveled several times in a single day; total distance traveled within a single day varied from 400 to 1,600 m (Giesen 1977).

By late summer, successful hens and their broods can be found using the same areas as the males and unsuccessful females. Brood mixing or shuffling often occurs at this time with two or three individual broods joining into a single flock known as a "gang" brood. Gang broods tend to remain separate from flocks of males but may be joined by unsuccessful females. All age and gender classes continue to use the high elevation summering areas into September when late summer or early fall snowstorms force them to move downhill into more protected areas (Braun 1969, Schmidt 1988). If the snow melts and weather conditions improve, birds may move back upslope. This pattern of movement may be repeated more than once before the birds completely abandon summering areas and gradually move downhill to wintering areas.

Habitat

General habitat description

White-tailed ptarmigan primarily inhabit alpine ecosystems at or above treeline (Braun 1971a, Braun et al. 1993). They also use stream courses and meadows within the subalpine zone (Braun 1971a, Braun et al. 1976; Herzog 1977, 1980). Alpine, as used in this document, refers to landscapes that occur at high elevations where trees are extremely dwarfed (krummholz) or can no longer grow. The term "tundra" is sometimes used interchangeably with alpine, but tundra more correctly refers to treeless landscapes that occur latitudinally beyond the limits where trees no longer can grow (Billings 1979). Both ecosystems are characterized by low temperatures, high winds, short growing seasons, and an absence of trees. However, in actuality, the similarities between alpine and tundra ecosystems are few because of considerable differences in radiation, moisture, topography, photoperiod, and soil conditions (Billings 1973, 1979). Alpine areas tend to be floristically richer than tundra environments. Alpine solar radiation is more intense. More snow falls in the alpine than in the tundra. The process of photosynthesis is disrupted at night in the alpine. In comparison, photosynthesis is continuous during the tundra summer when the sun never sets. Atmospheric pressure is lower in the alpine, topography is generally steeper, soils are shallower, and rocks are more abundant. Most importantly in regards to soils, permafrost is nearly absent in alpine ecosystems.

Alpine environments are among the most rigorous in the world. The extreme topography and climatic conditions prevalent in the alpine impose significant barriers to plant development. The alpine landscape is highly irregular, varying from sharp peaks and ridges, steep talus slopes, and rugged cliffs, to broad glaciated valleys, to gently rolling expanses hundred of hectares in size. Rocks are a prominent feature of most alpine areas although large expanses with few or no rocks are not uncommon. Rocks can vary from pebble-sized scree to house-size boulders and cover a few square meters or hundreds of hectares. Slopes range from nearly flat (less than 5 percent) to over 80 percent. Soils vary accordingly (Retzer 1956, Nimlos and McConnell 1965, Retzer 1974). Soils on high, convex, steep slopes are shallow, weakly-developed, coarse, and well-drained. Soils on lower, concave slopes and bottoms are deep, loamy, and poorly drained. Variations of these conditions occur in intermediate areas.

Following Wardle (1974), treeline occurs at an altitude where environmental tolerances of vascular plants, and in particular their ability to ripen their shoots to withstand seasonally adverse conditions, are abruptly reached. Moisture patterns, wind action, and temperature fluctuations all interact to influence where trees no longer can grow and the alpine begins (Zwinger and Willard 1972, Wardle 1974, Brown et al. 1978a, Billings 1979). Of these, none is more important in determining where treeline occurs than wind. Strong, persistent winds result in severe desiccation of exposed plant parts, especially during winter when little moisture is available because soils are frozen, as are the conducting channels in roots and stem bases (Zwinger and Willard 1972, Wardle 1974). Only a few species of trees and shrubs can survive in this environment, and everything growing in the alpine represents a dwarfed version of its counterpart at lower elevations. Larger plants simply cannot survive the exposure to the wind and cold. Trees appear more like shrubs. They become stunted, gnarled, and twisted, grow prostrate along the ground, and quickly disappear from the landscape with only a slight increase in elevation. Shrubs extend to higher elevations within the alpine zone than trees, but they also become increasingly dwarfed and restricted to protected areas with increasing elevation.

Where the climate is dry and continental, treeline is raised. In general, treeline decreases in elevation from south to north. In the western United States, treeline is about 3,500 m in New Mexico and southern Colorado, lowering to 2,900 m in central Wyoming and to 2,000 m in northern Montana (Zwinger and Willard 1972, Brown et al. 1978a). In Alaska, treeline occurs at around 1,000 m. The same pattern occurs along the coastal ranges. Treeline in the Sierra Nevada is approximately 3,200 m, diminishes to 2,900 m in northern California, to as low as 2,000 m in the North Cascades of Washington (Clarke and Johnson 1990).

Wind action not only influences where the alpine begins, but it also plays a major role in the distribution of plant communities within the alpine zone by influencing the distribution of moisture. Total annual precipitation in the alpine can vary from less than 63 to over 120 cm. Fall and early winter are the driest periods, with most of the precipitation occurring during late winter and early spring in the form of snow (Marr 1967). However, due to the effects of wind, this moisture is not evenly distributed. Many exposed alpine areas remain snowfree or retain little of the snow that falls, whereas protected sites not only retain the snow that falls on them but also catch snow blowing from more exposed sites.

Another significant factor affecting plant development in the alpine is the low heat budget (Brown et al. 1978a, Billings 1979). Much of the incoming solar energy is scattered or reflected back to the sky. This results in low growing season temperatures, periodic frosts during the growing season, and ultimately, a short growing season of only 60 to 90 days (Billings and Mooney 1968). Because of low temperatures and a short growing season, biological productivity in alpine environments is low (Scott and Billings 1964, Webber 1974). However, when expressed on a growing season basis, alpine plant productivity is comparable to other natural systems of herbaceous plants (Billings 1979).

Plant communities within alpine environments are frequently complex and extremely variable within short distances (Marr 1967). Alpine vegetation consists almost entirely of low growing perennial forbs, graminoids (grasses, sedges, and rushes), mosses, lichens, and dwarf shrubs (Marr 1967, Zwinger and Willard 1972, Billings 1979). Graminoids tend to be the most abundant and widespread plant forms in alpine communities. Annual plants are rare and contribute little to the vegetative cover or primary productivity. Most perennial plants have more living tissue below than above ground and their growth rate is relatively slow. Moisture is a major factor influencing plant distribution. Graminoids and low shrubs are dominant in wetter sites and cushion plants and lichens predominate on drier sites.

Alpine vegetation can best be described as a mosaic of many small plant communities that subtly intergrade with each other (Braun 1969). The floristic composition of these communities is remarkably uniform across broad geographic areas (Harrington 1964). Rydberg (1914) lists 250 vascular plant species as present in the Colorado alpine zone. Zwinger and Willard (1972) provide a comprehensive list of 862 plants that grow above treeline in the United States outside of Alaska and Hawaii. Of these, 359 are identified as occurring in the Southern Rocky Mountains. This probably closely approximates the number of plant species present within the range of white-tailed ptarmigan in Region 2. Major alpine plant communities of the Southern Rocky Mountains have been described in various detail by several investigators (Marr 1967, Eddleman 1967, Braun 1969, Zwinger and Willard 1972, May 1975). Although not present in all alpine areas, major alpine plant communities of the Southern Rocky Mountains can be generalized as *Kobresia* meadow, *Carex-Deschampsia* Meadow, *Carex-Geum* rock meadow, *Carex-Trifolium* turf, *Geum* turf, *Salix-Carex* wet meadow, *Trifolium* cushion plant fellfield, *Dryas* stand, and krummholz (*Picea*, *Abies*, *Pinus*, *Salix*) (Braun 1980).

Most of these plant communities are used by ptarmigan at sometime during the year (Braun 1971a), suggesting the species has a wide habitat tolerance within the alpine zone. However, certain habitat features must be present to insure continued use. Depending on time of year, the two most important features of all vegetation types used by white-tailed ptarmigan are presence of willow and rocky areas (Choate 1963; Braun 1971a; Herzog 1977, 1980; Frederick and Gutierrez 1992). The presence of willow is the key factor affecting ptarmigan distribution from late fall through early summer. During this time, willow is the primary source of food for ptarmigan (Weeden 1967, May and Braun 1972). Rocky areas near late-lying snowfields or other moist sites become important from mid-summer to early fall. These sites generally occur at higher elevations than areas used at other times of the year, but occasionally may be below or within the same areas used for breeding. Rocks provide protection from the weather and hiding cover from avian predators.

Johnson (1968) suggested that favorable ambient air temperatures for ptarmigan may be limiting and, therefore, a factor in determining habitat use patterns.

The classic example of this is when ptarmigan minimize the effects of colder night temperatures by moving to areas of soft snow to roost (Braun and Schmidt 1971). Less obvious is the role heat stress may serve in habitat selection. Ironically, in alpine environments, heat stress may be of greater importance than cold stress in influencing habitat use patterns (Zerba and Morton 1983, Wiebe and Martin 1998b). The reason is that ptarmigan are basically cold-adapted birds. They are not physiologically adapted to high ambient air temperatures. Consequently, they tend to seek microhabitats with cooler air temperatures. This can occur even during winter. On clear, warm winter days, ptarmigan will seek cover (shade) beneath coniferous shrubs or next to boulders to escape the direct and indirect (reflective) heat from the sun.

Choate (1963) reported that moist vegetation and rocks were common features associated with areas consistently used by ptarmigan in Montana. He further reported that timber, boggy areas, and shrubby vegetation over 46 cm tall were avoided. This latter finding is misleading because Choate (1963) only conducted his study from early June to mid-September when ptarmigan depend less on shrub-dominated communities. In another Montana study (Scott 1982), data collected from May to November indicated extensive use of shrub-dominated stream courses and krummholz stands of shrubs interspersed with stunted whitebark pine (*Pinus albicaulis*), subalpine fir (*Abies lasiocarpa*), and Engelmann spruce. Ptarmigan were observed sitting on, loafing and hiding under, walking through, and feeding on the ground among these trees.

In Alaska and British Columbia, where the three species of ptarmigan occur sympatrically, Weeden (1959) found that areas occupied by willow ptarmigan, rock ptarmigan, and white-tailed ptarmigan during the breeding season were progressively further above treeline. This segregation was related to features of the vegetation and terrain. Willow ptarmigan used areas of lush vegetation with high species diversity, where clusters of shrubs 1 to 2 m in height alternated with openings dominated by herbaceous vegetation less than 30 cm in height. The terrain was generally flat or moderate. Rock ptarmigan used areas slightly higher in elevation on more moderate slopes. The vegetation was similar in structure to areas used by willow ptarmigan but the shrubs were shorter (less than 1 m) and the herbaceous vegetation (openings) was more abundant but less diverse. White-tailed ptarmigan used the higher, steeper slopes characterized by ledges, cliffs, and rock out-croppings with narrow, vegetated shelves. Rock and boulder fields were abundant, and herbaceous plants were short, often covering less than 20 percent of the ground. Shrubs were rare, seldom exceeding 30 cm in height.

Breeding habitat

Breeding territories (**Figure 4**) are in areas of gentle to moderate slopes that become partially snow-free by mid-May and where willow is a major component of the plant community (Choate 1963, Braun 1971a, Herzog 1977, Frederick and Gutierrez 1992). The presence of willow and the availability of snow-free areas are considered the two most important factors influencing where ptarmigan breed (Braun 1971a, Schmidt 1988, Clarke and Johnson 1992). The elevational range of breeding areas varies depending on latitude, slope, and aspect. Ptarmigan breed at elevations from 1,219 to 1,542 m in Alaska, 1,280 to 2,650 m in British Columbia, 1,940 to 3,015 m in Alberta, 1,615 to 2,286 m in Washington, 1,915 to 2,499 m in Montana, and 3,350 to 4,250 m in Colorado (Braun et al. 1993). Early in the breeding season, most territories are situated near treeline and centered around stands of willows more than 0.5 m tall that protrude above the snow. As the snow melts and the vegetation "greens up," territories elongate uphill to include areas with more rocks, more herbaceous vegetation, and less willow. The willow tends to be shorter, and rocks typically exceed 25 percent of the cover and are larger than 30 cm in diameter (Braun 1971a).

Nesting habitat

Female ptarmigan nest on the ground within the boundaries of their breeding territories (**Figure 4**), generally in areas of moderate slope that become snow-free by early June (Braun 1971a, Braun and Rogers 1971, Giesen et al. 1980, Wiebe and Martin 1998b). Ptarmigan use a broad range of habitat types for nesting. Most nests have some type of cover immediately adjacent to the nest, usually in the form of rocks or clumps of vegetation. This cover is used primarily as protection against inclement weather and less for concealment (Giesen et al. 1980, Wiebe and Martin 1998b). For concealment, hens rely mainly on their cryptic plumage. Rock appears to be the preferred cover at nest sites because it offers greater protection from wind and snow than vegetative cover (Giesen et al. 1980, Wiebe and Martin 1998b), and presumably rock offers the best thermal environment for incubation (Wiebe and Martin 1997, 1998b). Although ptarmigan will nest in dense cover, such as willows and krummholz, they are more likely to nest in sites with less cover because of the increased risk of predation at

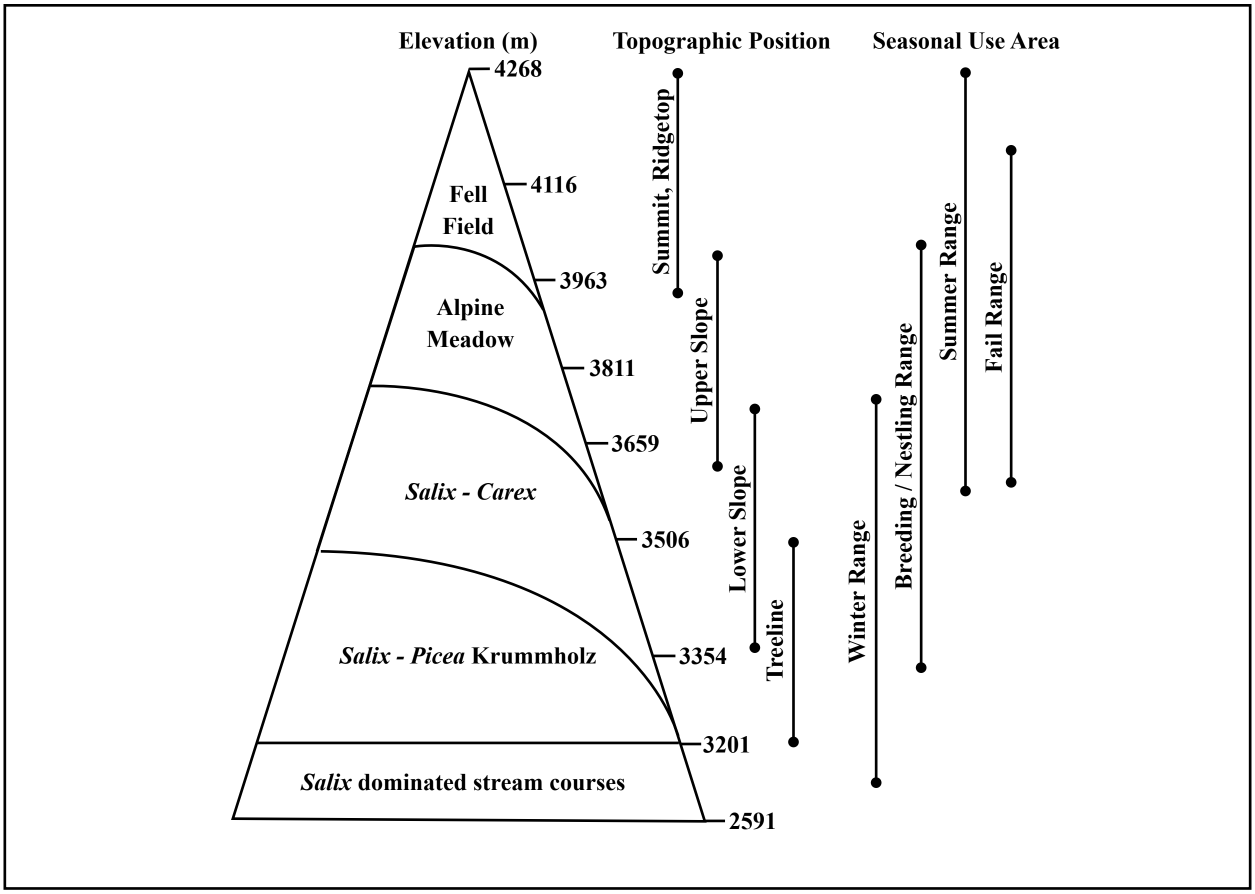

Figure 4. Approximate distribution of seasonal ranges of white-tailed ptarmigan within the Rocky Mountain Region (Region 2) of the U.S. Forest Service in relation to elevation, topographic position, and major alpine vegetation types. The actual distribution of seasonal ranges will vary depending on the aspect.

enclosed nest sites that offer few, unhindered escape routes (Wiebe and Martin 1998b).

Of 25 nests found in Colorado and described by Braun (1971a), 84 percent were located between 3,536 and 3,811 m elevation while 4 percent were below and 12 percent above this range. The 25 nests were in the following five cover types: krummholz (32 percent), *Carex-Geum* rock meadow (28 percent), *Geum-Carex-Trifolium* meadow (24 percent), *Geum-Poa* meadow (8 percent), and *Kobresia-Carex-Geum* meadow (8 percent). Braun (1971a) noted that most nests were protected from the wind either by being under shrubs or adjacent to rocks greater than 15 cm in diameter.

Giesen et al. (1980) reported site characteristics for 62 Colorado nests, including the 25 nests found by Braun (1971a). They speculated that most hens nested on the lower periphery of their mate's territory but provided no conclusive evidence to support this contention other than observational data. The median and mean slope measured at 60 nests was 20 and 21 percent, respectively, and ranged from 0 to 70 percent; 93 percent of the nests were on slopes less than 40 percent. There was no apparent selection for aspect; nests were located on south (32 percent), north (25 percent), west (23 percent), and east-facing (20 percent) slopes. Nest sites ranged in elevation from 3,383 to 3,901 m (median = 3,597 m, mean = 3,618 m). Twenty-five (40 percent) of the 62 nests were in rock or boulder fields, 20 (32 percent) were in turf or meadow situations, 11 (18 percent) were in evergreen krummholz, and six (10 percent) were in willow krummholz. Only one nest had no obvious protection from the wind. Most nests were protected either by rocks, clumps of grasses or sedges, willows, or spruce (krummholz). Nests in krummholz were located at the edge of the clump or adjacent to an opening within the clump to facilitate departure from the nest.

Using data collected over nine years in Colorado, Wiebe and Martin (1998b) described the attributes of 331 nest sites. The dominant cover type at nest sites included rock (45 percent), willow (33 percent), sedge

(17 percent), and conifer krummholz (5 percent). On average, conifer nests (mean overhead cover = 83 percent) were most concealed, followed by willow (62 percent) and rock (46 percent). Sedge nests had no overhead cover and the least lateral cover. The majority (54 percent) of nests faced east, the predominant aspect of the study area. Nearly half (49 percent) of the nests were on medium (12 to 24°) slopes, with 32 percent classified as steep (over 24°) and 19 percent as flat (less than 12°). The steepest nest site was situated on a 38° slope. Nest sites ranged in elevation from 3,467 to 4,161 m (mean = 3,725 m). Elevation of the nest was related to cover type and laying date. Rock nests had the highest mean elevation, followed by sedge, willow, and conifer. Elevation of the nest increased with laying date. Also, in years of early snowmelt, elevation of first nests was higher than in late years. The age of the hen was not a significant predictor of any nest site characteristic.

Wiebe and Martin (1998b) found that within seasons, cover type changed between first and second nest attempts. Compared to initial nests, renest sites were more often in rock and less often in willow or conifer cover types. Only 18 percent of females that initially nested in sedge and 16 percent that nested in willow renested in the same type; in both cases most (sedge = 82 percent, willow = 84 percent) hens that renested switched to rock. Conversely, 65 percent of the hens that initially nested in rock also used rock for their second nest attempt.

Summer and brood-rearing habitat

Brood-rearing areas for females and suitable summering areas for post-territorial males and unsuccessful females (**Figure 4**) occur on high, rocky, windswept ridges, benches, and mountain tops above the elevation of breeding territories (Braun 1971a). These areas usually center on late-lying snow fields, solifluction terraces (Knight 1994:208), or other moist sites, and are best described as a mosaic of rock fields and low growing vegetation consisting principally of *Carex* spp., *Polygonum* spp., *Trifolium* spp., and *Geum rossii*. Rocks commonly exceed 30 cm in diameter and comprise over 50 percent of the ground cover. Fellfields immediately adjacent to moist alpine meadows and areas of "patterned ground" caused by a process known as cryopedogenesis (Knight 1994:208) are important summer use sites for ptarmigan. Slopes on summering areas are moderate. Cliffs and steep slopes often occur nearby but are seldom used except for escape cover. Ptarmigan typically summer above 3,658 m elevation in Colorado, but they may summer as low as 3,506 m to as high as 4,268 m (Braun 1971a).

Braun (1971a) noted that in alpine areas grazed by domestic livestock there is no marked movement uphill to summering areas following the completion of breeding activities. Instead, birds move horizontally across the slope or downhill to rocky, wet areas within the willow and krummholz communities. This is especially true for females with broods. Males and unsuccessful females may move uphill, but depending on the intensity of the grazing, they may move back downhill or wander between suitable summering areas at higher elevations.

Fall habitat

Ptarmigan continue to use summering areas into early fall as long as weather conditions permit (Braun 1971a). With the first severe snowstorm, they move downhill to the upper edges of willow communities within the zone of breeding habitat (**Figure 4**). Some birds may move back to summering areas if the snow melts. By mid- to late fall ptarmigan are starting to molt to their winter plumage and favor areas with a patchwork of snow cover (Braun 1971a). These are usually the last areas to become snow-free in late summer and therefore, are one of the few remaining sources of green vegetation. Rocks are still a prominent feature of fall use areas. Sites used in the fall vary in plant species composition, but the most common plants include *Artemisia norvegica*, *Salix nivalis*, *Trifolium parryi*, *Geum rossii*, *Sibbaldia procumbens*, *Ranunculus* spp., *Carex* spp., and *Deschampsia caespitosa* (Braun 1971a).

Winter habitat

Partial segregation by gender occurs during the winter, with females wintering in large flocks near or below treeline and males wintering in small groups at higher elevations along the lower fringe of breeding areas (**Figure 4**; Hoffman and Braun 1977). Females move longer distances to wintering areas and congregate in larger numbers on wintering areas than males; this suggests that suitable wintering areas for females may be limited (Hoffman and Braun 1975, 1977). Both genders winter in areas dominated or co-dominated by willow (Braun 1971a, Braun et al. 1976, Herzog 1980, Giesen and Braun 1992). Areas used in winter typically are in drainage basins and along low ridges at or slightly above treeline (3,201 to 3,810 m) where food (willow) and roosting sites (soft snow) are readily available (Braun 1971a, Braun et al. 1976). Willow-sedge and krummholz alternately dominated by Engelmann spruce and willow are the two prominent vegetation types on wintering areas.

Portions of most wintering areas occur on northeast to southeast exposures that are somewhat protected from the prevailing winds (Braun et al. 1976). Large amounts of snow naturally accumulate on wintering areas due to their protected nature and presence of taller vegetation (willow and krummholz) that catches and holds blowing snow (Braun and Schmidt 1971, Braun et al. 1976). Wind action and its effect on snow deposition and hardness play a critical role in affecting the distribution of ptarmigan on wintering areas (Braun and Schmidt 1971). Because of wind action, willow bushes on exposed ridges are usually less than 1 m tall and are rarely snow covered. Such areas are consistently used as feeding sites throughout winter. During the day when ptarmigan are not feeding, they seek shelter beneath or on the lee side of dwarf conifers growing along ridges. However, snow on the ridges is often shallow and covered with a hard crust, making conditions unsuitable for night roosting. Consequently, at dusk the birds move from ridges to areas of deeper and softer snow along treeline or in bottoms where they can burrow beneath the surface (Braun and Schmidt 1971, Braun et al. 1976). At times they may use small openings below treeline for roosting at night.

Ptarmigan also feed and roost in willows growing in less exposed sites, such as along treeline and in drainage bottoms. Because of greater moisture availability and protection from wind, willows growing in this situation commonly exceed 1.5 m in height. Ptarmigan tend to avoid these sites in favor of low ridges during the early part of winter because the shrub cover is too tall and dense. However, as winter progresses and snow accumulates in these areas, the density and height of the willows above the snow decreases; this makes these sites more attractive to ptarmigan for both feeding and roosting. In conjunction with increasing snow depth, different portions of the willow plant become available to the foraging ptarmigan. By late winter and early spring, ptarmigan have access to younger shoots and buds on the tops of willows that earlier were unavailable to them.

Most known ptarmigan wintering areas in Region 2 occur at or above treeline (Braun et al. 1976). However, during severe winters and in some alpine ranges where willow communities above treeline are snow covered even during normal snowfall years, ptarmigan winter below treeline within the subalpine zone (Braun et al. 1976). While the majority of winter sites below treeline occur above 2,591 m, observations of ptarmigan in winter have been reported from as low as 2,348 m (Braun et al. 1976). Wintering areas below treeline are narrow and typically associated with stream courses. However, avalanche paths are used by ptarmigan in steeper mountain ranges. Wintering areas along stream courses can extend up to 10 km in length. These sites are typically dominated by willow, but alder (*Alnus*) and birch (*Betula*) may be co-dominants in localized areas. These shrubs commonly attain heights of 2 to 3 m and are rarely completely snow covered. Wind action is less extensive than above treeline; thus, suitable snow for roosting is readily available.

Nutrition and energetics

Food habits

The white-tailed ptarmigan is a characteristic herbivore of alpine environments. In the southern portion of its range, which includes Region 2, the white-tailed ptarmigan occurs allopatrically in relation to the other ptarmigan species. In the absence of competition with its congeners, white-tailed ptarmigan are able to exploit different resources, especially during winter, than it uses farther north (Weeden 1967; Moss 1973, 1974). Within Region 2, white-tailed ptarmigan consume a wide variety of foods including buds, twigs, catkins, fruits, seeds, flowers, stems, leaves, and insects (**Table 6**; Quick 1947, Weeden 1967, May and Braun 1972, Braun et al. 1993). The exact number of different species of plants consumed is unknown, but it probably totals less than 35; winter diets are the most restricted, and summer diets the most diverse (Weeden 1967, May and Braun 1972). Ptarmigan primarily forage on the ground by walking between foraging sites. During winter they frequently fly between suitable foraging and roosting areas (Braun and Schmidt 1971). They will perch in willow and alder bushes to obtain buds and catkins. Ptarmigan have been observed drinking water and eating snow (Warren 1916), but their need for water other than what is contained in the foods they eat is poorly understood (Braun et al. 1993).

May and Braun (1972) examined 286 crops from adult white-tailed ptarmigan collected from 16 localities in Colorado. They identified 26 different plants comprising more than 1 percent (aggregate dry weight of crop contents) of the diet. The number of different plant species consumed during each season was three in winter, five in spring, 18 in summer, and 16 in fall. Invertebrates made up less than 1 percent of the diet during any season, including summer. Some plants were consumed during more than one season. Except in the summer, willow was the most important food item in the diet of adult ptarmigan. In the winter, ptarmigan are nearly monophagous, with willow buds and twigs comprising 89 percent of the diet;

Table 6. Primary foods of male (M) and female (F) white-tailed ptarmigan in USDA Forest Service Rocky Mountain Region, expressed as percent of total dry weight of crop contents (compiled from May and Braun 1972 and May 1975). Sample sizes are listed in parentheses.

	Winter		Spring		Summer			Fall	
	M	F	M	F	M	F	Juvenile[1]	M	F
Food Item	**(14)**	**(44)**	**(16)**	**(10)**	**(24)**	**(13)**	**(8)**	**(104)**	**(61)**
Salix spp.	84	90	85	85	4	9		49	30
Dryas octapetala	15	3	5	1				1	3
Polygonum viviparum					2	54	32	22	16
Polygonum bistortoides					6	6			4
Potentilla diversifolia				4	3	3			1
Ranunculus spp.				4			4		
Saxifrage rhomboidea			1	1	7	4			1
Carex spp.					18	9		3	4
Trifolium spp.					13	4		3	7
Cerastium spp.					11			4	3
Geum rossii					6	4			
Oxyria digyna						1		3	2
Sibbaldia procumbens									3
Arenaria obtusiloba								2	3
Arenaria fendleri					3				
Antennaria spp.									3
Vaccinium spp.								5	1
Alnus tenuifolia		3							
Artemisia spp.					2				
Pedicularis spp.					1				
Heuchera parvifolia					1				
Lloydia serotina					1				
Androsace septenrionalis					3				
Grasses						2		2	7
Mustards					9			2	5
Invertebrates							63		

[1] For ptarmigan <5 weeks old. The diet of juveniles >5 weeks old is the same as adults.

mountain dryad (*Dryas octapetala*) and alder (*Alnus tenuifolia*) are winter foods of secondary importance. In the spring, ptarmigan continued to rely heavily on willow (85 percent) along with the green leaves and flowers of mountain dryad, varileaf cinquefoil (*Potentilla diversifolia*), snowball saxifrage (*Saxifrage rhomboidea*), and buttercup (*Ranunculus* spp.). Major foods during the summer included the seeds and leaves of alpine bistort (*Polygonum viviparum*), sedges, clovers, willow (6 percent), American bistort (*P. bistortoides*), mouse-ear chickweed (*Cerastium* spp.), snowball saxifrage, alpine avens, and unidentified mustards (Brassicaceae). Willow (43 percent) was the principal food eaten during the fall, with the leaves and seeds of alpine bistort, clovers, mouse-ear chickweed, sedges, and fruits of blueberries (*Vaccinium* spp.) eaten before they became unavailable due to increasing snow depths.

May and Braun (1972) found that males and females ate the same foods but in different amounts depending on the season (**Table 6**). Males consumed more mountain dryad than females during the winter and into early spring prior to pair formation. This was attributed to the partial segregation of genders from early winter through early spring. Mountain dryad was available in greater amounts on the higher, windswept slopes where males wintered. During the summer, males used a greater variety of plant species and consumed less alpine bistort and more sedges and clovers than females. Bulbils of alpine bistort comprised 54 percent of the crop contents of females during the summer compared to only 2 percent for males. In the fall, both genders consumed chiefly willow and alpine bistort; however, males consumed more of both species than females because females included a greater variety of foods in their fall diet compared to males.

Weeden (1967) identified the contents of 167 white-tailed ptarmigan crops collected from 23 locations in Colorado, Wyoming, Washington, Alaska, British Columbia, and Alberta. The leaves of *Salix* and *Ranunculus*, *Dryas* flowers, grass and sedge seeds, and *Polygonum* fruits were common items found in the limited sample of spring and summer crops. His analysis of 73 crops from Colorado produced similar findings as May and Braun (1972), with willow, mountain dryad, and alpine bistort being the most common items identified. The only food item identified by Weeden (1967) not reported by May and Braun (1972) was alpine laurel (*Kalmia polifolia*).

Weeden (1967) also found regional differences in the diet of white-tailed ptarmigan. He specifically noted the lack of berries in the fall diet of ptarmigan in Colorado compared to Alaska and British Columbia. This finding was confirmed by the work of May and Braun (1972) who only found use of berries in one area in Colorado where ptarmigan remained near treeline during the summer and fall and ate berries of *Vaccinum*. Weeden (1967) further noted that during the winter white-tailed ptarmigan in Alaska ate more alder catkins and less willow compared to ptarmigan in Colorado. Ptarmigan in Alaska also ate birch. May and Braun (1972) found limited amounts of alder and no birch in the diet of ptarmigan in Colorado. The differences were attributed to greater amounts of alder in Alaska and competition for food among the three species of ptarmigan on wintering areas in Alaska. Throughout its range in Alaska, the white-tailed ptarmigan occurs sympatrically with willow or rock ptarmigan or both. In these situations, rock ptarmigan feed heavily on birch, lightly on willow, and rarely on alder; willow ptarmigan feed heavily on willow, lightly on birch, and rarely on alder; and white-tailed ptarmigan consume all three shrubs but feed most heavily on alder (Weeden 1967; Moss 1973, 1974).

Coniferous species, such as Engelmann spruce, subalpine fir, lodgepole pine (*Pinus contorta*), whitebark pine, and bristlecone pine (*Pinus aristata*), are regionally and locally abundant in areas where white-tailed ptarmigan winter. However, Quick (1947) is the only investigator who has reported the use of conifer needles as winter food. He found that subalpine fir needles comprised up to 10 percent by weight of winter droppings of ptarmigan in Colorado. Although Quick (1947) visually documented ptarmigan feeding on willow, he never mentions observing them feeding on subalpine fir. May and Braun (1972) collected crop samples in some of the same areas examined by Quick (1947), but their results did not confirm any use of subalpine fir. Likewise, conifer needles were not identified in any of the crops examined by Weeden (1967).

Choate (1963) documented white-tailed ptarmigan food habits in Glacier National Park, Montana by following and observing the birds' use of different plant species and plant parts. He made no attempt to quantify use and only mentioned the main foods eaten. New shoots of mountain heather (*Phyllodoce* spp. and *Cassiope* spp.) and mosses were preferred foods in the spring. Buds and flowers of snow willow (*Salix nivalis*), lanceleaf springbeauty (*Claytonia lanceolata*), and alpine (mountain) buttercup (*Ranunculus eschscholtzii*) were important food items in the summer. In the late summer and fall, snow willow leaves and stems, sedge and grass seed heads, and *Mimulus* spp. leaves were the principal foods of ptarmigan. Once snow accumulated, ptarmigan used tall willows and heather protruding above the snow, and mosses and dwarf willow that remained exposed.

Clarke (1991) studied the summer foraging strategies of a native (Rocky Mountain National Park, Colorado) and an introduced (Sierra Nevada, California) population of white-tailed ptarmigan. Birds in the introduced population consumed 14 different plant species; arctic willow (*Salix anglorum*) and sedges were eaten by all ptarmigan and together comprised 99 percent g dry weight of the average diet. In Rocky Mountain National Park, ptarmigan consumed 18 different plant species. Alpine avens was used by all ptarmigan and comprised 35 percent g dry weight of the average diet; other major foods included alpine clover (*Trifolium dasyphyllum*), alpine bistort, and mountain dryad.

Salt (1984) made cursory observations of the feeding habits of white-tailed ptarmigan in Alberta. He reported that willow, sedges, heaths, along with some common wildflowers such as buttercups and fleabanes (*Erigeron* spp.), and a variety of insects were the most important foods of these birds. Salt (1984) mentions observing ptarmigan at mats of juniper polytrichum moss (*Polytrichum juniperinum*), but he was unable to confirm that they were actually eating this plant.

Invertebrates, and to a lesser extent grasses, appear to be minor items in the diet of adult white-tailed ptarmigan. Species of grasses widely distributed in alpine habitats that seldom showed up in the diet of ptarmigan included several species of bluegrass (*Poa* spp.) and tufted hairgrass (*Deschampsia cespitosa*). Invertebrates may be of greater importance to young ptarmigan (<5 weeks) than adults (May 1975, Salt 1984, Braun et al. 1993); however, no detailed studies have been conducted on the food habits of young ptarmigan. May (1975) reported that the crop contents from eight ptarmigan less than 3 weeks old consisted primarily of invertebrates (63 percent dry weight), but plant foods, especially alpine bistort, also were consumed in large quantities. May (1975) noted that by 5 weeks post-hatch the diet of young ptarmigan closely resembled that of adults.

Ptarmigan, as well as other gallinaceous species, ingest small stones that accumulate in the gizzard. These small stones are referred to as grit and are necessary to assist in the mechanical abrasion of coarse or hard foods to facilitate digestion and possibly as a source of minerals (May and Braun 1973). Grit was present in the crops examined by May and Braun (1972) during all seasons of the year. They identified, weighed, and measured gizzard stones from 288 adult white-tailed ptarmigan collected at 16 locations in Colorado. They found that mean grit size was largest during the winter months and smallest in July. Females retained a significantly greater mean annual amount of grit than males. The amount of grit fluctuated around a relatively constant mean value of 3.54 g for males and 3.96 g for females from September through March. The amount of grit then declined steadily for males until June and then increased sharply in July and August to reach the September level. For females, the amount of grit increased markedly from April to its highest level in June, decreased dramatically in July, and increased again in August. The grit was predominantly a mixture of quartz and associated feldspars (orthoclase and plagioclase), with quartz being the most preferred. Amphiboles, pyroxenes, micas, rhyolite, and andesite also were present in limited amounts, depending on where the gizzards were collected.

Seasonal changes in grit size were correlated with dietary changes. Coarse foods, such as the buds, twigs, and leaves of willow, are eaten most often from September through June. Accordingly, mean grit size was largest during this period. Grit size was smallest during July and August, which are the only months when soft, succulent, green vegetation, and not willow, is the primary food of ptarmigan. The adaptive significance of female ptarmigan having more gizzard stones than males is unknown. The likely explanation is that the additional grit provides needed minerals for laying. However, May and Braun (1973) rejected this theory based on the argument that quartz, the primary type of grit, is hard, wears slowly, and contains little calcium. These characteristics make quartz an efficient food grinder but an unlikely source of minerals.

It is well documented that different species of grouse internally regulate the length of their ceca to compensate for changes in food quality (Leopold 1953, Moss and Hanssen 1980, Remington 1989), and white-tailed ptarmigan are no exception. May (1975) found the mean lengths of the combined ceca of white-tailed ptarmigan were longest during the winter (males = 723 mm, females = 735 mm) and shortest during the summer (males = 643 mm, females = 671 mm). May (1975) argued that the ceca were longer in the winter to allow for the digestion of more highly fibrous foods (buds and twigs) eaten by ptarmigan at this time of year. Since May (1975) conducted his study, there has been conflicting evidence as to the exact function of the ceca in grouse (Remington 1989). In accordance with May (1975), several investigators (McBee and West 1969, Moss and Hanssen 1980, Sibly 1981) have proposed that the ceca primarily function as fermentative and absorptive reservoirs that allow for the digestion of highly fibrous foods. Others (Fenna and Boag 1974, Remington 1989) hypothesize that the major function of the ceca is to permit sorting of intestinal contents and to allow for rapid excretion of poorly digestible components and retention of more digestible components. It is likely that ceca serve both functions, but its primary function appears to be one of food partitioning (Remington 1989). Regardless, both theories can be used to explain why the ceca are longer during winter.

Energetics

Alpine environments offer growing conditions that produce particularly nutritious forages (Webber 1974). The short, cool growing season favors rapidly maturing plants. This rapid growth is associated with high nutritive quality in plant tissue. In addition, alpine areas are exposed to longer periods of solar radiation than low elevation sites due to the lower angle of the horizon. Longer days allow for longer periods of plant growth and accumulation of plant nutrients, and brief, cool nights result in minimum nutrient losses to respiration. As a consequence, nitrogen and carbohydrate levels in alpine plants remain higher for longer portions of the day than plants growing at lower elevations (Webber 1974). The quality of light in alpine regions also is somewhat higher than that at lower elevations. The atmosphere is thinner in alpine regions, allowing more of the sun's energy to reach the earth's surface and become available to plants.

May (1975) measured the caloric content of eight of the most common foods (willow, mountain dryad, buttercup, alpine bistort, American bistort, sedge, alpine avens, and clover) consumed by ptarmigan in Colorado. On average, the available energy contained in the buds, twigs, catkins, and leaves of willow (range = 4.76-5.25 kcal g^{-1} dry weight) was higher than the energy available from the leaves, flowers, seeds, and bulbils of herbaceous plants (range = 3.92-5.00 kcal g^{-1} dry weight). Within individual foods, available energy differed by plant parts. For example, energy availability was greater in willow buds and twigs compared to leaves and catkins. More energy also was available in flowers and fruits than leaves of herbaceous plants.

White-tailed ptarmigan in Alaska digest about 40 to 45 percent of their winter food and metabolize 2.3 to 2.7 kcal g^{-1} dry weight (Moss 1973). The winter diet of these birds includes alder, birch, and some willow. Ptarmigan inhabiting the contiguous United States, on the other hand, feed almost exclusively on willow. For this reason, May (1975) assumed that the digestibility and metabolizable energy of willow eaten by Colorado ptarmigan was 45 percent and 2.25 kcal g^{-1} dry weight, respectively. The estimated daily metabolizable energy intake of Alaskan white-tailed ptarmigan during the winter was 105 kcal per day; their existence metabolism was calculated to be 100 kcal per day. These data suggest that the diet of white-tailed ptarmigan during winter is more than adequate to maintain body condition.

This conclusion is further substantiated by data presented by May (1975), which shows that white-tailed ptarmigan gain body mass over winter. Males are heaviest (mean = 383-412 g) from November to January before starting to lose weight in late winter and spring. They are lightest in June (mean = 344-353 g) towards the end of breeding activities and then steadily gain weight from July through January. Females attain their greatest weight in June (mean = 415-447 g) during egg laying and weigh the least in July (mean = 353-360 g) following incubation. Females gain weight from July to December, lose weight slightly in January, and gradually gain weight through June. Although ptarmigan gain body mass over the winter, their overall body fat levels remain low, generally averaging less than 3 percent (range 1-6 percent) throughout the year (Braun 1971b, May 1975, Braun et al. 1993). Body fat measured as percent of dry tissue is highest for males in the fall (3.5 ± 1.1 SD) and lowest in the spring (1.4 ± 0.7 SD). In comparison, body fat of females is at its highest level in the spring (6.1 ± 4.5 SD) and at its lowest level in the fall (1.0 ± 0.4 SD). Apparently white-tailed ptarmigan have sufficient food supplies and obtain enough energy from these foods so that they do not need to build fat reserves to make it through periods of poor food quality or quantity (Braun 1971b).

Studies using doubly-labeled water indicate that the field metabolic rate between May and July for white-tailed ptarmigan (mean mass = 368 g) living above 3,600 m elevation ranges from 206 to 442 kJ per day and averages 326 kJ per day ± 28 SD (Thomas et al. 1994). Comparatively, white-tailed ptarmigan have a field metabolic rate only 81 percent of that predicted for non-passerine birds of similar size (Nagy 1987). The low metabolic rate can be attributed to a variety of behavioral, morphological, and physiological adaptations designed to conserve energy (Martin et al. 1993). White-tailed ptarmigan have a wide thermoneutral zone (Johnson 1968), walk rather than fly (Martin et al. 1993), use snow roosts (Braun and Schmidt 1971), develop feathered tarsi and toes in winter to facilitate walking on snow (Höhn 1977), select microhabitats to maximize metabolic efficiency (Martin et al. 1993), and generally live a sedentary lifestyle. In addition, ptarmigan have counter-current exchange mechanisms that reduce circulation and decrease heat loss from sitting and walking on the snow. Ptarmigan also change colors, which alters the absorptive and reflective properties of the feathers. Thus, changing colors is an adaptation to climatic conditions (Walsberg 1983), as well as being associated with predator avoidance.

The standard metabolic rate calculated for captive white-tailed ptarmigan in spring is 48.8 kcal per 24 hr (Johnson 1968). This is higher than expected based on predictive equations and is believed to reflect the additional energy required for molting (Johnson 1968). Mean body temperature has been measured at 39.9 °C (Johnson 1968) and 39.5 °C (May 1975). The thermoneutral zone where little or no energy needs to be expended to control body temperature ranges from 6 to 38 °C (Johnson 1968). The Lower Critical Temperature of 6 °C is exceptionally low for birds and is most likely due to the low conductance (high insulation value) of the ptarmigans' plumage (Veghte and Herreid 1965, Johnson 1968). Ptarmigan have one of the lowest evaporative efficiency estimates recorded in birds (Lasiewski et al. 1966, Johnson 1968). Even at high ambient temperatures, ptarmigan can evaporate no more than 90 percent and usually only about 60 percent of their metabolic heat (Johnson 1968). Consequently, ptarmigan are highly susceptible to heat stress.

Demography

Reproductive performance

Subadult males are physiologically capable of breeding provided they are successful in establishing a territory and attracting a female to the territory their first year (Braun and Rogers 1971, Schmidt 1988, Braun et al. 1993). All females are believed to breed in their first year and attempt to lay at least one complete clutch per nesting season (Giesen et al. 1980, Braun et al. 1993). Non-breeding females are rarely encountered (May 1975, Schmidt 1988, Braun et al. 1993). Both adult and subadult females will lay a replacement (renest) clutch if their first clutch is lost or abandoned during laying or the early stages of incubation (Giesen and Braun 1979c). Renesting rates can vary from 0 to over 80 percent. There are only a few documented cases of white-tailed ptarmigan attempting to renest more than once in a single nesting season. The probability of laying a replacement clutch is highest for older females (Wiebe and Martin 1998a, Sandercock et al. 2005a). The probability of renesting also is greater in normal compared to harsh years when the spring snowmelt is delayed (Martin and Wiebe 2004). Giesen and Braun (1979b) estimated that renesting occurred in at least eight of 12 years on their study area in Rocky Mountain National Park, Colorado and accounted for 11.5 percent of all (*n* = 156) marked broods observed.

White-tailed ptarmigan and spruce grouse (*Falcipennis canadensis*) lay the smallest clutches of any North American grouse (Bergerud 1988). Average clutch size of first nests for white-tailed ptarmigan is five to six eggs and ranges from four to eight (Choate 1963, Giesen et al. 1980, Braun et al. 1993, Wiebe and Martin 1998a). Mean clutch size of first nests for adults (6.2 eggs ± 0.7 SD) is larger than for subadults (5.8 eggs ± 0.9 SD) (Braun et al. 1993). However, mean sizes of renest clutches are similar between age classes (adults = 4.8 eggs ± 0.7 SD, subadults = 4.6 eggs ± 0.9 SD); renest clutches are also smaller than first clutches (Braun et al. 1993).

Hatching success (percent of all eggs laid that hatch) of 838 eggs from 153 clutches on Mt. Evans, Colorado averaged 33.6 percent (Braun et al. 1993). Embryo viability (percent of eggs incubated to completion) for the same population was 88 percent based on 323 eggs from 61 clutches. This is identical to the embryo viability reported by Giesen et al. (1980) for 177 eggs from 34 nests located throughout Colorado. Giesen et al. (1980) did not provide any estimate of hatching success.

Several investigators have reported estimates of nesting success (percent of all clutches initiated that hatch at least one egg) for white-tailed ptarmigan (Braun and Rogers 1971, Giesen et al. 1980, Clarke and Johnson 1992, Wiebe and Martin 1998a, Martin and Wiebe 2004). It is clear from these studies that nesting success varies among years and among areas within the same year primarily due to differences in weather (Choate 1963, Clarke and Johnson 1992, Martin and Wiebe 2004). Younger ptarmigan differ from older ptarmigan in that they lay smaller clutches, nest later, and renest less frequently, but despite these differences, nesting success does not appear to vary with age (Wiebe and Martin 1998a, Sandercock et al. 2005a).

Generally, birds that breed in alpine habitats are at a disadvantage because the breeding window is short. In late years when snow melt is delayed, nest failure can be high with little or no opportunity for renesting. Such is the case with white-tailed ptarmigan. Although white-tailed ptarmigan have strong coping mechanisms for dealing with climatic extremes, when snowmelt is extremely delayed, nesting success is greatly reduced (Clarke and Johnson 1992, Martin and Wiebe 2004). Nesting success on Mt. Evans for first nests during the harsh year of 1995 was only 9.4 percent compared to 38 percent over several normal years (Martin and Wiebe 2004). During 1995, the spring snowmelt was delayed 3 weeks until late June compared to the other 8 years of study when snowmelt dates ranged from 4 to 31 May (Martin and Wiebe 2004). Nesting success for an introduced population of white-tailed ptarmigan in the Sierra Nevada, California ranged from 19 to 61 percent and was negatively correlated with spring snow depth (Clarke and Johnson 1992). Nesting success averaged 56.7 percent for 60 nests located over a 12-year period in Colorado from 1966 to 1977 (Giesen et al. 1980). Yearly samples were too small to compare annual variation in nesting success.

Some studies have estimated nesting success for white-tailed ptarmigan based on the proportion of females located with and without broods. This approach often produces an inflated estimate of nesting success because hens with broods are easier to locate than hens without broods. In addition, hens that lose their entire brood soon after hatching may be misclassified as unsuccessful (failed to hatch a clutch of eggs). Using this approach, Braun and Rogers (1971) reported the following estimates of nesting success for five different areas over a 4-year period in Colorado: 40 to 75 percent (Rocky Mountain National Park and Mesa Seco), 35 to 75 percent (Crown Point), 25 to 50 percent (Mt. Evans), and 25 to 75 percent (Independence Pass). Choate (1963) found that the percentage of hens with broods varied from 35 to 82 percent over four years of study in Glacier National Park, Montana. Both Braun and Rogers (1971) and Choate (1963) attributed the annual differences in nesting success to weather conditions.

Perhaps the most meaningful measure of reproductive performance is fledging success, which is the percent of all eggs laid that produce young surviving to the stage where they become independent (8 to 10 weeks) of the brood hen. No studies have measured fledging success in white-tailed ptarmigan to this stage of development. However, Braun et al. (1993) reported an estimate of fledging success at Mt. Evans of 14.2 percent for 809 eggs to 25 days post-hatch; brood success was approximately 33.8 percent, with 45 of 133 females rearing at least one chick to 25 days of age. In the Sierra Nevada, California, brood success (measured as the percent of hens producing at least one chick that survived until late August) ranged from 16 to 52 percent (Clarke and Johnson 1992). Wiebe and Martin (1998a) found that older females raise more chicks (mean = 0.73 chicks/female) to independence than younger females (mean = 0.38 chicks/female). Overall, the proportion of hens that lose their entire brood averages about 32 percent and is greater for younger (45 percent) than older (15 percent) females (Martin et al. 1993).

Braun and Rogers (1971) reported that regardless of nesting success and timing of peak of hatch, in most years, average brood size by 1 September did not vary greatly from one year to the next. In their study, average brood size between 16 and 31 August 1966 to 1968 on selected study areas throughout Colorado was 4.2, 4.0, and 3.5 chicks per brood, respectively; the odd year was 1969 when brood size averaged only 2.9 chicks. On Niwot Ridge located in Colorado's northern Front Range, May (1975) detected slightly greater variation in late August brood sizes ranging from 3.0 to 4.4 chicks per brood over a four year period (1971-74). Average brood size during late August in Rocky Mountain National Park was 3.9 (1975) and 3.8 (1976) chicks per brood (Giesen 1977). In Montana, brood size at flight age (10 to 14 days) varied from 3.25 to 3.47 from 1959 to 1962 (Choate 1963). This was nearly two chicks per brood less than ascertained for broods in Colorado for approximately the same period (Braun and Rogers 1971, May 1975, Giesen 1977). Clarke and Johnson (1992) calculated a median (and mode) brood size for white-tailed ptarmigan in the Sierra Nevada, California of four chicks from 1982 to 1987. They did not clarify when the counts were obtained. In another Sierra Nevada study, Frederick and Gutierrez (1992) reported an average late August brood size of only 2.0 chicks per brood. However, this estimate was based on the observation of just three broods over two years.

Productivity or breeding success, expressed as the percentage of juvenile grouse in the fall population, has been estimated for white-tailed ptarmigan populations in Colorado (Braun and Rogers 1971, May 1975), Montana (Choate 1963), and California (Clarke and Johnson 1992, Frederick and Gutierrez 1992). Productivity varies annually in accordance with differences in nesting success and chick survival. Braun and Rogers (1971) suggested that productivity must be at least 40 percent to maintain population levels. In Colorado, productivity ranged from 20.0 to 60.5 percent on five different areas over three or four years and exceeded 40 percent in 12 (67 percent) of 18 cases (Braun and Rogers 1971). On another Colorado study area, May (1975) reported percent gains of 54.5 (1971), 40.9 (1972), 15.2 (1973), and 36.8 percent (1974). Productivity at Logan Pass, Montana exceeded 40 percent (range = 46.9-90 percent) every year from 1959 to 1962 (Choate 1963). Clarke and Johnson (1992) defined breeding success as the number of juveniles in the fall divided by the number of breeding birds in the spring. Their estimates of breeding success for a study site in the Sierra Nevada, California ranged from 17 to 80 percent between 1982 and 1987. Using the same approach as Braun and Rogers (1971), May (1975), and Choate (1963), their estimates of productivity would range from 14 to 45 percent and exceeded 40 percent in only one of six years of data collection.

Predation

Grouse die from many causes including accidents, starvation, disease, hunting, and predation, but of these causes, predation accounts for over 85 percent of all reported mortalities in grouse (Bergerud 1988). Biologically, it has long been understood that the ultimate fate of most grouse is to be depredated and eaten by some predator. For this reason, predation is a major force shaping the dynamics of grouse populations (Bergerud 1988, Reynolds et al. 1988, Hewitt et al. 2001, Schroeder and Baydack 2001).

The contention of most biologists is that predation is not a limiting factor for grouse populations provided suitable habitat is available. Grouse have evolved with predators and have developed strategies to compensate for high predation rates. However, in many areas, man's activities over the past century have dramatically altered the landscape and apparently disrupted the balance between predators and prey in ways that favor certain predators. For example, raccoons (*Procyon lotor*), striped skunks (*Mephitis mephitis*), and red fox (*Vulpes vulpes*) now have more diverse food supplies (e.g., grain, garbage, road kills, domestic poultry) and places to rear their young (e.g., abandoned buildings, barns, haystacks). In addition, predators such as common ravens (*Corvus corax*), common crows (*C. brachyrhynchos*), golden eagles (*Aquila chrysaetos*), and great horned owls (*Bubo virginianus*) have more places to nest and perch in the form of trees planted by man and artificial structures built by man. In essence, man's activities have contributed to an increase in some predator populations, allowed other predators to expand their range into previously unoccupied areas, and improved the hunting efficiency of still other predators.

Fortunately for white-tailed ptarmigan, man's impacts on alpine landscapes have, for the most part, been localized. Consequently, the balance between predators and prey has remained relatively intact. Because the alpine is an exceptionally harsh environment, the suite of prey species and corresponding predators is significantly less than in other landscapes. Some of the major predators of grouse nests at lower elevations, such as snakes, skunks, raccoons, and ground squirrels, are absent or rare in the alpine. Furthermore, during the winter, when ptarmigan are concentrated on small areas and potentially most vulnerable to predation, avian predators are least abundant in the alpine. The principal predators of ptarmigan include prairie falcons (*Falco mexicanus*), golden eagles, long- and short-tailed weasels (*Mustela frenata*, *M. erminea*), coyotes (*Canis latrans*), and red foxes (Braun et al. 1993). American marten (*Martes americana*) also are suspected predators of ptarmigan (Salt 1984). Eggs are taken by common ravens, foxes, weasels, mountain lions (*Felis concolor*), and coyotes (Braun et al. 1993). In addition to eating eggs, common ravens also may take ptarmigan chicks (Braun et al. 1993).

Predation accounted for approximately 80 percent of all known mortalities during a 4-year study on five areas in Colorado (Braun and Rogers 1971). Of 35 documented predation events, 74 percent were attributed to avian and 26 percent to mammalian predators. Prairie falcons and red foxes were identified as the primary avian and mammalian predators, respectively. In another Colorado study, predators destroyed 166 of 248 (67 percent) ptarmigan nests where the fate could be ascertained; first (63 percent) and second (68 percent) nests were equally vulnerable to predation (Wiebe and Martin 1998b). About 67 percent of the nest predation events occurred at night between 2230 and 0430 hours and were attributed to predators that hunt by scent (mammals) rather than sight (avian) (Wiebe and Martin 1997). The main nocturnal predators were long-tailed weasels, coyotes, and red foxes. Giesen et al. (1980) identified coyotes and weasels as primary nest predators, and they documented at least one nest being depredated by corvids. Braun et al. (1993) reported that of 107 depredated nests, 16 percent were taken by avian predators, 16 percent by mammalian predators, and 68 percent by unknown predators.

Although losses of white-tailed ptarmigan nests, young, and adults to predation can be high (Braun et al. 1993), overall predation rates on white-tailed ptarmigan are low compared to other grouse species (Bergerud 1988). Braun and Rogers (1971) speculated that the success of avian predators in taking ptarmigan is probably low. Bergerud (1988) also postulated that low mortality rates of white-tailed ptarmigan can be explained on the basis of low predation from raptors. First, there are fewer avian predators that hunt in the alpine, especially during winter. Second, two potentially effective avian predators on ptarmigan, gyrfalcons (*Falco rusticolus*) and peregrine falcons (*F. peregrinus*), are rare or absent in most alpine areas within the southern range of the white-tailed ptarmigan. Third, white-tailed ptarmigan occur at relatively low densities in scattered patches of suitable habitat compared to other prey species. Thus, no avian predator can afford to be specialized for white-tailed ptarmigan. Finally, ptarmigan are inconspicuous, seldom fly unless approached within a few meters, and only move when feeding, making them exceptionally difficult to detect by predators that rely on vision to locate prey.

White-tailed ptarmigan respond to avian predators by crouching near or under rocks and remaining motionless (Braun and Rogers 1971). If pursued by an avian predator, ptarmigan will run a short distance then fly uphill and land in a rocky area and hide. Despite their reluctance to fly, ptarmigan are strong fliers and can out-fly most raptors, especially flying uphill. In the presence of mammalian predators, ptarmigan remain motionless but very alert; they will fly if pursued. Female ptarmigan perform distraction displays by feigning injury to lure predators away from their nest or concealed chicks (Schmidt 1988, Braun et al. 1993). In addition, females as well as males may try to intimidate potential predators by performing attack displays where they run directly at the predator hissing loudly with head raised, eyecombs extended, and wings spread laterally to expose the white carpal patches (Schmidt 1988, Braun et al. 1993). During the breeding season, the male is highly vigilant in the presence of his mate; this allows the female to forage more efficiently before and during incubation (Artiss and Martin 1995, Artiss et al. 1999). Females will retrieve eggs displaced within 18 cm from the nest (Giesen 1978). The obvious adaptive advantage of this behavior is that it insures their continued incubation, but more importantly, it may increase survival of the hen and her remaining clutch, as eggs outside the nest may attract predators.

Survivorship

While longevity records for free-living white-tailed ptarmigan include a female of 12 years and a male of 15 years (Braun et al. 1993), the average life span of a white-tailed ptarmigan for non-hunted or lightly hunted populations is about three years (Choate 1963, Braun 1969, May 1975). Survival rates depend on age class, gender, and level of hunting activity (Choate 1963, Braun 1969, May 1975, Braun et al. 1993). They tend to be higher for males than females after their first year, lower for younger (less than 1 year old) and older (greater than 4 years old) grouse, and significantly reduced in heavily hunted populations but not in lightly hunted populations (**Table 7**). The average annual survival rate for an unhunted population of white-tailed ptarmigan in Rocky Mountain National Park was 56 percent (Braun 1969); this was similar to the 58 percent survival reported by Choate (1963) for an unhunted population in Montana. Survival rates in one moderately hunted (Crown Point) and one heavily hunted (Mt. Evans) population in Colorado were approximately 40 percent and 30 percent, respectively (Braun 1969). Survival (58 percent) in a lightly hunted population on Niwot Ridge was comparable to survival in the unhunted populations (May 1975). Survival of adults in an introduced population on Pikes Peak averaged 63 percent and consistently exceed 55 percent (range =

Table 7. Survival estimates by age and gender reported by Braun (1969) and May (1975) for unhunted (Rocky Mountain National Park, RMNP), lightly hunted (Niwot Ridge, NR), and heavily hunted (Mt. Evans, ME) populations of white-tailed ptarmigan in Colorado.

Location and Age Class	Male Survival (percent)	Female Survival (percent)
RMNP		
Year 1 (1st autumn-1st spring)	31	45
Year 2 (1st spring-2nd spring)	76	45
Year 3 (2nd spring-3rd spring)	74	70
Year 4 (3rd spring-4th spring)	60	56
Year 1-4	47	49
Year 2-4	71	53
NR		
Year 1	41	41
Year 2	88	73
Year 3	76	67
Year 4	81	50
Year 1-4	62	53
Year 2-4	81	68
ME		
Year 1	35	51
Year 2	16	27
Year 3	51	17
Year 4	50	0
Year 1-4	31	40
Year 2-4	22	24

57-76 percent), with males (65 percent) surviving at a slightly higher rate than females (60 percent) (Hoffman and Giesen 1983).

Survival is lowest during the early spring and fall when ptarmigan are moving from and to wintering areas (Braun and Rogers 1971). Most females (88 percent), and even a greater percentage of males (97 percent), survive the breeding season (Braun et al. 1993, Martin et al. 1993). Winter is the longest season for ptarmigan, but proportionally, daily survival during the winter is probably greatest than during any other season because predator densities, particularly raptors, are lowest at this time of year.

Several factors may contribute to the lower annual survival of females. Foremost, they move longer distances than males (Hoffman and Braun 1975, Giesen and Braun 1993). Also, females with chicks may be more vulnerable to predation than males during the summer because they are more conspicuous while attending the chicks and do not have the security of associating in flocks with other mature ptarmigan. That is, their ability to detect predators may be less than for birds in flocks. While some females are killed on the nest, nesting does not appear to be a major cause of mortality in females. Wiebe and Martin (1998b) found that although nest predation rates are high (over 60 percent), few (9 percent) females are actually killed on the nest. Even so, nesting increases the vulnerability of females to predation beyond that experienced by males.

Choate (1963) estimated that the survival of chicks from time of hatch to fledging was 56 to 65 percent, and the survival of immature (juveniles) birds was 37 percent from fall to spring. Observations of 49 marked broods in Rocky Mountain National Park indicated that chick survival approached 66 percent during the first two weeks of life (Giesen 1977). Once the chicks reached two weeks of age, survival was nearly 90 percent until brood breakup (Giesen 1977). Braun and Rogers (1971) presented data showing 70 to 80 percent survival of chicks during the first two weeks following hatch for broods observed throughout Colorado. Still other data presented by Braun et al. (1993) indicated much lower survival (42 percent, 115 of 276 chicks from 58 broods) of chicks during the first three weeks following hatch than previously reported. Giesen and Braun (1993) reported that the minimum September to June survival rate of banded juvenile males was approximately 35 percent.

Competition

Rock ptarmigan, willow ptarmigan, and blue grouse have distributions that overlap that of white-tailed ptarmigan at certain times of the year. In the northern portion of its range, white-tailed ptarmigan directly compete for resources during winter with rock and willow ptarmigan (Weeden 1959). Competition for food in winter was one reason given why white-tailed ptarmigan in Alaska and British Columbia feed more on alder and birch and less on willow than white-tailed ptarmigan further south where rock and willow ptarmigan are absent (Weeden 1967). No other instances of competition with rock and willow ptarmigan have been reported, nor are there any documented cases of hybridization (Braun et al. 1993).

Male blue grouse establish territories and female blue grouse occupy spring home ranges along treeline where they likely occur in close proximity to ptarmigan. In addition, female blue grouse with broods sometimes venture into the alpine and may come in contact with ptarmigan. Blue grouse have hybridized with several other grouse species, but the white-tailed ptarmigan is not one of them (Zwickel 1992). Furthermore, it is unlikely that blue grouse and ptarmigan directly compete for resources. In early spring when ptarmigan are still feeding on willow, blue grouse are primarily eating conifer needles. Blue grouse also eat more insects and berries when available than ptarmigan. Blue grouse will eat willow, but willow has not been identified as a major food item in most studies of blue grouse (Zwickel 1992). Although blue grouse and ptarmigan can be found using the same areas at the same time of year, more often they use different portions of the alpine at different times. For example, when blue grouse broods frequent the alpine in summer, they commonly occur at lower elevations than the rocky ridges and mountain tops used by ptarmigan. Because blue grouse depend on the shrubs and krummholz for cover when using alpine habitats, they seldom venture beyond the upper limits of where willow grows.

Rocky Mountain elk (*Cervus elaphus nelsoni*), which have increased in abundance dramatically throughout their range, are a potential competitor with white-tailed ptarmigan. In Colorado, there has been a corresponding increase in the use of alpine habitats by elk during all seasons, including winter. In Rocky Mountain National Park alone, elk wintering in the alpine increased from 29 in 1933 to over 300 in 1976

(Stevens 1980). Hobbs et al. (1981) estimated that about 25 percent of the elk's diet in upper montane habitats during winter in Rocky Mountain National Park is comprised of willow. Data collected by Braun et al. (1991) indicate that willow cover in subalpine and alpine areas in Rocky Mountain National Park decreased from 1971 to 1989, a period when elk numbers within the park were increasing. They hypothesized that heavy use of willow by elk in early winter and early spring may constrain ptarmigan breeding densities by reducing the amount of willow protruding above the snow that would normally be available to ptarmigan in late winter and early spring. This also may be happening elsewhere, but the effects probably are most pronounced in alpine areas where elk are typically not hunted and allowed to graze undisturbed.

Another potential competitor of white-tailed ptarmigan is the moose (*Alces alces*). Historically, moose were rare within the range of white-tailed ptarmigan in Region 2 (Kufeld 1994). Moose were transplanted into North Park near Rand, Colorado in 1978 and 1979, into the Laramie River drainage north of Rocky Mountain National Park in 1987, and in southwestern Colorado near Creede from 1991 to 1993. In 2004, moose were released on the Grand Mesa near Grand Junction, Colorado. Kufeld (1994) estimated the statewide population in 1994 at 740 moose. Management objectives are to allow the southwest population to grow to 350 animals and to maintain the North Park/Laramie River population at 450 to 525 animals (Kufeld 1994). In Colorado (Kufeld and Bowden 1996), as well as in many other areas (reviewed by Peek 1997, Renecker and Schwartz 1997), moose use willow extensively for both food and cover; this may bring them in direct competition with ptarmigan. Even though moose consume willow, alder, and birch (Renecker and Schwartz 1997), Boer (1997), in discussing interspecific relationships of moose, did not mention competition with ptarmigan. The only habitat use study conducted on moose in Colorado suggests that most willow-dominated habitats used by moose occur below treeline (Kufeld and Bowden 1996). Thus, currently, moose in Colorado likely have minimal contact with ptarmigan except possibly during the winter along stream courses below treeline. Moose may eventually exploit more of the willow communities at or above treeline. If moose and elk both use these areas, the combined effects could have negative consequences on ptarmigan food availability.

Mountain goats, which were first introduced into Colorado in 1948, may be yet another competitor with white-tailed ptarmigan. Their populations have since grown in size and distribution due to natural expansion and additional transplants. At the time mountain goats were first introduced, they were considered non-native to the state. In 1993, the International Order of Rocky Mountain Goats proposed that the mountain goat be declared a native species in Colorado. The Colorado Wildlife Commission passed this resolution in March 1993 despite overwhelming evidence that mountain goats are not native to Colorado (Gross et al. 2000). Mountain goats also were introduced in Wyoming, but they do not occur within the limited area occupied by white-tailed ptarmigan.

Mountain goats are highly adaptable and well suited to using a variety of plant communities within alpine and subalpine zones (reviewed by Gross et al. 2000); they eat many of the same plants as ptarmigan. Although they are more of a grazer than browser, they do consume browse, such as willow (Dailey 1981), which places them in direct competition with ptarmigan. Goats also feed on many of the same sedges and forbs consumed by ptarmigan during summer (Dailey 1981). In the Olympic Mountains, Pike (1981) documented that saxifrages and bistorts, which May and Braun (1972) found to be important summer and fall foods of white-tailed ptarmigan, were heavily affected by grazing of introduced mountain goats.

Rocky Mountain bighorn sheep are native to Region 2 and use many of the alpine ranges occupied by ptarmigan. However, because the bighorn sheep that live in alpine habitats are primarily grazers and feed mostly on graminoids (Dailey et al. 1984), they are less of a potential competitor with ptarmigan than elk, moose, or mountain goats. Furthermore, whereas elk and mountain goats may remain in the alpine year-round, bighorn sheep frequently winter at lower elevations within the montane zone.

Parasites, diseases, and toxins

Documented cases of disease and parasite infections in white-tailed ptarmigan are low (Braun and Willers 1967, Haskins 1969, Braun and Rogers 1971, Braun et al. 1993). Rates of infection vary by age class and season, but no deleterious conditions have been noted (Braun and Rogers 1971, Braun et al. 1993). Only 16 (5 percent) of 300 ptarmigan surveyed for blood parasites were positive (Stabler et al. 1971, 1974), 101 (22 percent) of 455 had coccidia (Stabler et al. 1979), four (2 percent) of 204 had nematodes (Olsen and Braun 1971), and five (4 percent) of 130 had cestodes (Olsen et al. 1978). Hermatozoa infection in white-tailed ptarmigan may be the result of contact with the more heavily parasitized blue grouse (Stabler et al. 1974).

Parasite infections in ptarmigan are believed to be natural and not responsible for any substantial mortality (Braun and Rogers 1971). Even so, the potential for population impacts should not be dismissed because disease outbreaks in grouse may easily go undetected (Braun et al. 1994a). There are cases where parasite infections have been documented to impact grouse populations. For example, parasites are known to cause significant mortality in red grouse (*Lagopus lagopus scoticus*), a subspecies of willow ptarmigan (Hudson 1992). However, red grouse are intensively managed through habitat manipulation and predator control, and they are maintained at un-naturally high densities, which may make them more susceptible to infection.

Cadmium is a highly toxic element found naturally in low concentrations in most soils. However, in a 10,000 km^2 region of central and southwestern Colorado known as the ore belt, cadmium is much more common due to the impacts of mining (Larison et al. 2000, Larison 2001). Mines release cadmium through runoff from waste and tailing piles and from adits; the runoff moves the cadmium downstream where it is deposited in wetlands, making it available for uptake by plants. All plants take up cadmium, but willow is one of the few plants that biomagnify it, up to two orders of magnitude above background concentrations (Larison et al. 2000). These wetland areas are preferred wintering sites for female ptarmigan (Braun et al. 1976), thereby exposing them to heavier doses of cadmium than males through their winter diet of willow. Once consumed, cadmium bioaccumulates in the kidneys and contributes to irreversible renal tubular damage (Larison et al. 2000, Larison 2001). Cadmium-induced renal failure has been shown to affect calcium balance and structural integrity (Larison 2001). The damaged kidneys excrete calcium year-round. Eventually the source of this calcium drain is bone, which weakens and becomes brittle. Females are not only exposed to higher doses of cadmium, but they also are more sensitive to its effects because of their high demand for calcium during egg laying. Mortality rates for older females living within the Colorado ore belt have been found to be significantly higher than for females living outside the ore belt (Larison et al. 2000, Larison 2001). Due to the exceptionally high mortality of older females, sex ratios in the adult segment of the population within the ore belt are highly skewed (1 female:2.3 males) in favor of males; thus, over 50 percent of the males may be unmated (Larison et al. 2000, Larison 2001).

Population regulation

Several intrinsic (i.e., spacing behavior) and extrinsic factors (i.e., weather, disease, food, habitat, predation), either singly or in combination, have been suggested to influence survival and reproduction in various species of grouse (Angelstam 1988, Hannon 1988). Long-term studies of hunted and unhunted populations of white-tailed ptarmigan in Colorado indicate that breeding densities fluctuate widely among years, with no clear evidence of population cycles (Braun et al. 1993). Choate (1963) speculated the primary controlling mechanism for the white-tailed ptarmigan population on his study area in Montana from spring through fall was weather and its impact on production. Wang et al. (2002a,b) provided additional evidence that weather is a key factor in the demography of white-tailed ptarmigan populations. They found that local climatic variables, but not large-scale climatic patterns, affected the population dynamics with 1-year lags of white-tailed ptarmigan in Rocky Mountain National Park. The time-lagged effects were believed to be due to the impacts of local weather conditions on reproduction and recruitment.

May and Braun (1972) ruled out food as a limiting factor for populations of white-tailed ptarmigan in Colorado during any season. They used weight data to show that white-tailed ptarmigan rarely undergo food shortages, because changes in weight are correlated with behavioral traits and not with changes in availability of food (May and Braun 1972, May 1975). Braun et al. (1993) citing other sources (Braun and Rogers 1971, Braun and May 1972) and unpublished data stated that annual survival of adults, spring body condition, and recruitment of juvenile white-tailed ptarmigan are not greatly influenced by predation, disease, parasites, or environmental constraints. Although factors such as hunting (Braun and Rogers 1971), habitat degradation by large ungulates (Braun et al. 1991), and pollution (Larison et al. 2000, Larison 2001) may reduce breeding densities in some areas, Braun et al. (1993) contended that these factors are not general phenomena that regulate populations.

May (1975) predicted that long-term trends in breeding densities of white-tailed ptarmigan populations in Colorado should be stable with periodic fluctuations around mean densities. The fluctuations would result from good and bad production years caused by weather conditions during the spring and summer. May's (1975) prediction is based on the premise that the number of ptarmigan breeding territories that an alpine area can support is relatively fixed because of the stability of alpine environments. In other words, there are only so many areas where ptarmigan can breed in the alpine, and the quantity and quality of these areas remain fairly constant between years. Thus, the opportunity for large population increases is limited by the stable environment in which the ptarmigan lives (i.e., change occurs slowly and habitat manipulation is usually not a viable option). This is in sharp contrast to habitats occupied by species such as ruffed grouse, blue grouse, and sharp-tailed grouse (*Tympanuchus phasianellus*) where the same block of habitat subjected to manipulation can go from supporting few grouse to supporting many grouse in a short time. The opportunity for large population increases is further limited because, compared to other grouse species, white-tailed ptarmigan produce relatively few young, even in a good production year, and turnover in the breeding population is low (Sandercock et al. 2005b).

Using long-term data sets for rock and willow ptarmigan, Bergerud et al. (1985) evaluated the following two hypotheses to explain annual changes in numbers of breeding ptarmigan: (1) fluctuations are caused by density-dependent changes in the mortality of birds over 4 months old that are excluded by territorial behavior, and (2) populations fluctuate through annual changes in breeding success measured as juveniles per adult in the fall population. Their analyses of 11 populations showed that changes in the size of the breeding population were positively correlated with breeding success during the previous season. However, Watson and Moss (1987) argued that the main mistake in the analyses conducted by Bergerud et al. (1985) was to infer that such correlations conclusively demonstrated that breeding success caused changes in breeding numbers. They provide evidence showing that changes in breeding success alone are not sufficient to explain the dynamics in population size.

The controversy over what influences stability in animal populations is basically between those who argue that control occurs through extrinsic factors and those who argue that control occurs through intrinsic factors. In the past, these two theories were considered mutually exclusive, but biologists are now attempting to describe how they interact to regulate populations (Watson et al. 1998). Clearly, despite several long-term studies of grouse (reviewed by Boag and Schroeder 1992, Zwickel 1992, Schroeder and Robb 1993), including white-tailed ptarmigan (Braun et al. 1993), the exact mechanisms of population regulation remain unclear and continue to be a subject of debate among biologists.

Population model

Sandercock et al. (2005a) developed an age-structured matrix model to examine age-dependent variation in 11 demographic parameters for female white-tailed ptarmigan in Colorado (**Table 8**). Age-specific variation in ptarmigan demography was primarily due to components of fecundity related to egg production. In essence, clutch size and probability of renesting increased with female age (**Table 8**). Female ptarmigan that were 2 years of age or older produced first clutches that were 0.5 eggs larger on average than 1-year old females. A greater proportion of 3-year old females renested after loss of first and second clutches. Three-year old females laid more eggs per year than 1-year old females; 2-year old females were intermediate. Despite these age-specific differences in egg production, the stochastic effects of nest and brood predation resulted in similar rates of annual fecundity (female fledglings per breeding female per year) among 1, 2, and 3+-year old females (**Table 8**).

Apparent survival rates were highest for 2-year old females, but they did not significantly differ from survival of 1-, and 3+-year old females. Sensitivity and elasticity values indicated that changes in the survival of 3+-year old females would have the greatest impact on the finite rate of population change (λ) in white-tailed ptarmigan. Estimates of λ predicted a declining population. However, demographic rescue via dispersal maintained the population (Martin et al. 2000). If the population was effectively closed, then the annual survival rate would need to be adjusted by + 38 percent to obtain an λ = 1. The average generation time was 2.62 years ± 0.40 SD (95 percent CI = 2.05-3.62 years). The stable age distribution was weighted towards 3+- year old females (0.474 ± 0.069 SD), with fewer 2- (0.194 ± 0.033 SD) and 1- (0.333 ± 0.041) year old females.

The relatively high survival rates of white-tailed ptarmigan apparently buffer against potential effects of perturbations on reproduction (Sandercock et al. 2005b). In general, white-tailed ptarmigan are well-adapted to the alpine environment, and extreme variations in climatic conditions have little effect on survival of females (Martin and Wiebe 2004). Nonetheless, factors that increase the mortality of older females are most likely to have the greatest impact on white-tailed ptarmigan populations. Such factors are more likely to be human-caused than natural. For instance, global warming (Wang et al. 2002a), differential harvest of older females (Smith and Willebrand 1999), and accumulation of contaminants in female body tissues

Table 8. Demographic parameters for 1, 2, and 3+- year old female white-tailed ptarmigan breeding in the vicinity of Mt. Evans, Colorado during 1987 and 1989-1997. Data from Sandercock et al. (2005a) expressed as means ± 1SE or frequency.

Demographic parameter	1 year	2 years	3+ years
Clutch size (1st nest)	5.6 ± 0.1	6.1 ± 0.1	6.3 ± 0.2
Clutch size (renest)	4.7 ± 0.2	4.8 ± 0.2	5.0 ± 0.2
Percent nest success (1st nest)[1]	32.4	40.0	32.4
Percent nest success (renests)	38.7	33.3	31.8
Probability of renesting once	0.417	0.414	0.69
Probability of renesting ≥ 2 times	0.000	0.000	0.25
Percent hatching success[2]	85.2 ± 4.1	86.0 ± 3.6	80.0 ± 5.5
Percent fledging success[3]	66.7	61.1	77.8
Percent fledglings/chick hatched[4]	62.8 ± 5.3	56.2 ± 10.1	64.5 ± 9.3
Apparent survival[5]	0.423 ± 0.059	0.643 ± 0.105	0.465 ± 0.087
Adjusted survival[6]	0.581	0.884	0.639

[1] Probability that at least one egg hatched and produced a chick that left the nest.

[2] Proportion of eggs laid that hatched and produced chicks that left the nest.

[3] Probability that at least one chick survived until 15 to 25 days after hatching.

[4] Proportion of hatched chicks that left the nest that survived until fledging at 15 to 25 days.

[5] Annual probability that a female survived and returned to the study area.

[6] Adjusted survival rate that would yield a stationary population ($\lambda = 1$) if combined with observed age-specific variation in components of fecundity.

(Larison et al. 2000) could all result in higher mortality of older females.

CONSERVATION

Conservation Status of White-tailed Ptarmigan in Region 2

Populations of white-tailed ptarmigan in Region 2 are stable and in no immediate jeopardy of declining. However, this does not negate the importance of Region 2 in the rangewide conservation of the species. On the contrary, Region 2 is perhaps the single most important region within the USFS system with regards to conservation of white-tailed ptarmigan. Region 2 supports the largest population of white-tailed ptarmigan in the world outside of Alaska and contains the greatest expanse of suitable habitat for this species within the contiguous United States.

With few exceptions, white-tailed ptarmigan complete their entire life cycle above treeline. Therefore, probably no other species is better suited as an indicator of the health of alpine ecosystems. Region 2 contains some of the most accessible white-tailed ptarmigan habitat throughout the species' range, and much of this habitat occurs in close proximity to major human population centers. Consequently, the potential for human-related impacts on white-tailed ptarmigan are arguably greatest in Region 2. For these reasons, the white-tailed ptarmigan should be considered a species of special concern and afforded high conservation status in Region 2.

Threats

General

All species of grouse have their strongholds in natural ecosystems (Storch 2000, Schroeder et al. 2004). Therefore, maintaining healthy grouse populations requires large, relatively undisturbed, natural landscapes. Although some grouse species can tolerate a moderate degree of habitat disturbance and can use and benefit from artificially created habitats, most healthy grouse populations are primarily associated with extensive natural landscapes exposed to natural disturbance regimes (Storch 2000, Schroeder et al. 2004). The white-tailed ptarmigan is probably one of the grouse species least tolerant to habitat disturbances because it occupies a very stable and extremely fragile environment that can take decades, if not centuries, to recover from disturbance.

Opportunities for protection and management of white-tailed ptarmigan are greater than for any other grouse in the United States because most (over 90 percent) of the habitat is under public ownership administered by the USFS, Bureau of Land Management (BLM), and National Park Service (NPS). There is little state or privately owned land in the alpine. Thus, the kind and extent of management of alpine ecosystems, and consequently white-tailed ptarmigan, in the western United States, including Region 2, is mainly a reflection of the policies of the USFS, BLM, and NPS.

The alpine ecosystem evolved in the absence of man, and without man, these systems are capable of persisting almost indefinitely (Billings 1973). To say that alpine ecosystems are "fragile" means that they are highly susceptible to anthropogenic disturbances; otherwise, they are one of the most stable and hardy systems in the world (Billings 1973). The best management practice for alpine systems is to leave them alone. Alpine ecosystems are among the most difficult to restore following disturbance (Brown et al. 1978a, Brown et al. 1978b, Brown and Johnston 1979, Chambers 1997, Macyk 2000). Rates of recovery are slow and directly related to the severity of disturbance (Chambers 1997). Man has had limited success enhancing or restoring alpine communities.

Human impacts within the alpine zone in North America are relatively recent and not as widespread as in other life zones. The severe environment and low productivity within the alpine zone have been deterrents to human use and habitation. Only within the last 150 years has modern man brought his industrial, agricultural, and recreational activities to these regions. As of 1976, Brown et al. (1978a,b) estimated approximately 12 percent (343,800 ha) of the alpine landscape in the western United States had been disturbed due to human activities. The major causes of disturbance in order of area disturbed were grazing (75 percent), recreation (11 percent), mining and mineral exploration (10 percent), roads (4 percent), pipelines (<1 percent), power lines (<1 percent), and reservoirs (<1 percent).

An early effort to identify problems of North American grouse only mentions grazing as a threat to white-tailed ptarmigan (Hammerstrom and Hammerstrom 1961). Braun (1980) listed grazing, mining, recreation, and manipulation of alpine watersheds as major threats to alpine avifauna, including white-tailed ptarmigan. The Status Survey and Conservation Action Plan for Grouse identifies the following activities as possible threats to white-tailed ptarmigan: road construction, mining, snow catchment fences, ski area development, pollution near urban areas, over-grazing by domestic livestock, hiking, developments that result in increased abundance of generalist corvid, canid, and mustelid predators, and over-harvest (Storch 2000). Wang et al. (2002b) warned of the possible effects of climatic warming on the dynamics of white-tailed ptarmigan populations. Braun et al. (1993) citing Braun and Rogers (1971) and Braun et al. (1976) state that localized distribution of white-tailed ptarmigan can be affected by road construction, water reservoirs, mining, construction of snow catchment fences, microwave relay stations, off-road vehicles, overgrazing by domestic livestock, ski area developments, and over-harvest. All of these factors, except over-harvest, are believed to impact ptarmigan largely by reducing the abundance and distribution of willow.

Rigorous collection of data concerning the impacts of human activities on white-tailed ptarmigan populations is lacking, but information does exist on the impacts of various human activities on alpine plant communities. This information has been used for making inferences about the impacts of these activities on ptarmigan. For example, any activity that significantly reduces the distribution or abundance of willow at or above treeline within the range of ptarmigan will likely have a negative impact on ptarmigan. However, no data have been collected to assist biologists in predicting the extent of impact of human activities on ptarmigan populations. This information is vitally needed not only for ptarmigan, but all species of grouse, and it must be collected and evaluated through designed experiments (Braun et al. 1994b). Biologists are scrambling to obtain this information on other species and subspecies of grouse where habitat loss, degradation, and fragmentation have reduced historic distributions by over 50 percent (Storch 2000, Schroeder et al. 2004). Entire populations have disappeared, and some subspecies and even species of grouse are on the verge of extinction (Storch 2000).

Although the white-tailed ptarmigan currently occupies nearly all of its historic range, there is still reason for concern. Steady increases in human populations will eventually place more demands on alpine environments, which could have catastrophic impacts on the welfare of ptarmigan populations. For this reason, threats to white-tailed ptarmigan should be taken seriously. Because recreation may be an issue in one area, grazing in another, and mining somewhere else, it would be easy for biologists and land managers to minimize the threats as local issues with no major impacts at the state or regional level. This type of thinking is dangerous. Biologists and land managers must broaden their perspective and consider the cumulative impacts of threats to ptarmigan populations when formulating management strategies.

Grazing

Livestock grazing is the dominant land use within the occupied range of white-tailed ptarmigan in the United States outside of Alaska. Sheep are the principal domestic livestock using alpine ranges because cattle are poorly adapted to using this environment (Alexander and Jensen 1959, Thilenius 1975). Sheep numbers peaked in the western United States about 1910 (Stoddard and Smith 1955). According to Wasser and Retzner (1966), there were over 300 sheep allotments and 40 cattle allotments partially using alpine rangelands in Colorado and Wyoming in 1959. This was 20 percent fewer sheep allotments and 37 percent fewer cattle allotments than existed 20 years earlier. Until this time, many alpine ranges were used continuously for summer grazing (Thilenius 1975). Herding practices were negligent and involved grazing sheep in tightly grouped bands and continuously bedding them in the same area, usually near water, for several consecutive nights. Trailing, over-grazing, and trampling have all resulted in considerable damage to alpine habitats (Paulsen 1960, Bonham 1972). Long-term use and improper herding have had a significant impact on the structure and composition of many alpine areas, to the extent that it is difficult to determine the "natural" state of these areas (Thilenius 1975).

Because of the lack of information concerning comparative physiological responses to grazing among alpine plant species and their competitive interactions, the management of alpine grazing systems remains largely empirical (Tieszen and Archer 1979). Range management principles and practices used in other ecosystems must be carefully considered and evaluated before they are applied to alpine habitats (Thilenius 1979). Many portions of the alpine are simply unsuited for grazing by domestic livestock (Thilenius 1975). Wet areas are important as aquifers, and vegetation growing in these areas is susceptible to trampling. Drier sites have low herbage production and high erosion potential. Slopes over 40 percent must be avoided regardless of plant coverage because it is doubtful that they can be grazed without damage. Even on areas that could be grazed, there are few good indicators for assessing range readiness, measuring forage utilization, or assessing range condition and trends (Thilenius 1975). Finally, and perhaps most importantly, the greatest danger in grazing alpine ranges is the long time span needed for misused ranges to recover (Thilenius 1975).

Sound grazing management promotes the use of forage resources while having a neutral or positive impact on plant vigor. Proper livestock grazing should maintain or enhance desirable plant communities, improve vegetation palatability, increase native plant diversity, and promote residual cover. There is minimal evidence to suggest that grazing in alpine ranges accomplishes any of these objectives. In addition, range management practices that are designed to increase forage production for livestock (e.g., reseeding, applying herbicides and fertilization) have negative, unsuccessful, or inconclusive consequences when applied to alpine ranges (Scott and Billings 1964, Billings and Mooney 1968, Thilenius et al. 1974, Thilenius 1975, Bear 1978). Fertilization and herbicide treatments both favor graminoids at the expense of forbs. Forbs are of greater importance to ptarmigan as food than grasses, especially during the summer and fall (May and Braun 1972).

Any activity that reduces the forb component of plant communities in areas used by ptarmigan during the summer and fall will have negative consequences to the species. This includes grazing by sheep. Some of the most important foods identified in the diet of sheep on alpine ranges are clovers and bistorts (Strasia et al. 1970). May and Braun (1972) found that bistorts and clovers comprised 41 and 27 percent (dry weight) of the summer and fall diets of white-tailed ptarmigan. Alpine bistort alone comprised 54 percent of the summer diet of female white-tailed ptarmigan (May and Braun 1972). Comparison of grazed and ungrazed alpine hairgrass meadows showed that palatable forbs, such as bistorts and buttercups, were more abundant in ungrazed areas, and unpalatable species, such as western yarrow (*Achillea lanulosa*), were more abundant in grazed areas (Bonham 1972). Yarrow is not an important food for ptarmigan, but bistorts and buttercups are (May and Braun 1972).

Grazing by wild ungulates also may negatively impact alpine habitats. Elk herds have grown dramatically due to greater protection and enforcement of game laws and lack of natural predators. Hunting has been mostly ineffective as a means of population control. The problem is not conservative regulations, but the inability to achieve desired harvest levels on private lands. Elk use of alpine ranges has increased during all seasons of the year, especially where they are not hunted.

Mountain goats, more so than any other wild ungulates, tend to use alpine areas year-round. Based on sound scientific evidence, this species is not native to the area occupied by ptarmigan in Region 2 (Gross et al. 2000). The establishment and subsequent expansion of mountain goat populations have raised concern about their potential impacts on native animals and plants within the alpine ecosystem. The concern mainly has been about competition with bighorn sheep, but ptarmigan also may be affected by the introduction of mountain goats.

Moose are native to portions of Region 2, but historically they were rare or absent within the occupied range of ptarmigan in Region 2. Moose have been transplanted to several sites in Colorado. Because of their extensive use of willow communities, moose may have the greatest potential for impacting ptarmigan if their populations continue to increase and expand. However, currently they make limited use of alpine willow basins and do not pose an immediate threat to ptarmigan in Region 2.

Recreation

Whereas grazing of alpine lands by domestic livestock has declined, recreational use has markedly increased. It has been nearly 28 years since Brown et al. (1978b) identified recreation as one of the fastest growing causes of disturbance to alpine lands. They reported roughly 38,000 ha of alpine disturbance in the western United States caused by recreational activities including trail, campsite, and trampling disturbances and another 12,748 ha of disturbance due to permanent and unimproved roads and off-road vehicle use. Brown et al. (1978b) considered the estimates of all types of disturbance provided in their publication to be conservative.

Today, recreational activities, in the form of hiking, camping, off-road vehicles (including snowmobiles), fishing, hunting, back-country skiing, downhill skiing, mountain biking, rock climbing, nature viewing, and photography, continue to be major uses and causes of disturbance in alpine areas. An example of the increase in recreational activity in alpine areas is the use of Colorado's "fourteeners." Ebersole et al. (2002) presented data on the use of trailheads that provide access to 14,000 ft. (4,364 m) peaks in the Leadville Ranger District of the Pike-San Isabelle National Forest. The data indicated a 10 to 25 percent increase in use per year during the 1990's. At these rates, use was doubling every three to seven years. Hesse (2000) estimated that roughly 75,000 persons ascend the "fourteeners" in Colorado annually, with "fourteeners" along the Front Range receiving as many as 500 ascents on a single weekend in July and August.

Trampling is the primary destructive outcome of hiking in the alpine. Willard and Marr (1970, 1971) found that some areas and certain plant forms are more vulnerable to modification by trampling than others. Generally, the vulnerability to damage is directly related to the moisture conditions of the soil; the wetter the soil the greater the potential for damage. Sedges of wet areas are most susceptible to trampling, cushion plants of fellfields are moderately resilient, and sedges and grasses of turf stands are most resilient (Willard and Marr 1970). Although trampling may be confined to a relatively small area next to a road (scenic overlook) or along a trail, the damage often extends to a larger area due to erosion from wind and water.

Where many people concentrate their walking in a small area, damage to alpine areas can take place in one to two weeks. Observations made over a 4-year period in Rocky Mountain National Park of areas protected from trampling showed almost complete recovery of vegetation that had been trampled for only one season (Willard and Marr 1971). In another area subjected to trampling for 26 years, an increase in vegetation growth was documented, but the dominant species had reduced vigor and some of the other important species normally found in the plant association were absent after four years of protection. In still another area that had been severely damaged during 38 years of trampling, there were no signs of recovery after four years of protection. Willard and Marr (1971) predicted that some alpine areas damaged by only a few seasons of human activity may require hundreds of years, possibly even a thousand years, to rebuild a natural and persistent (climax) plant community.

Purchase of full-size 4-wheel drive vehicles and other off-road vehicles, including motorcycles, snowmobiles, and all-terrain vehicles, for recreational purposes has increased dramatically. Flather and Cordell (1995) predicted that by 2010 the number of people in America driving motor vehicles off road will increase 108 percent. In the past, 4-wheel drive vehicles were primarily purchased for use as work vehicles, with recreational use being of secondary importance. Today, 4-wheel drive vehicles are common in rural as well as suburban western American households. The same is true for other off-road vehicles. The manufacturing and sale of off-road vehicles has become a thriving industry that continues to grow. Although off-road vehicles are used for many purposes, their primary use is recreational. Off-road vehicles, other than motorcycles, are relatively recent forms of motorized transportation that have facilitated use of areas previously inaccessible to most people. The classic example of an off-road vehicle that has permitted this to happen is the snowmobile. Snowmobiles first appeared on the commercial market in 1962. In 1969, 290,000 snowmobiles were placed on the consumer market along with over 50,000 all-terrain vehicles and 400,000 trail bikes (Doan 1970). By 1974, snowmobile sales in North America had grown 2,500 percent, with nearly 400 models produced by over 50 different companies (Ives 1974).

The extent of use and damage to alpine areas by 4-wheel drive and off-road vehicles has been poorly documented. Erosion, slumping, soil compaction, vegetation damage, noise pollution, and harassment of wildlife have all been identified as environmental impacts of off-road vehicle use (reviewed by Lodico 1973). There is no evidence that ptarmigan abandon sites frequented by motorized vehicles, but they may temporarily move if disturbed, and occasionally ptarmigan are killed by collisions with motorized vehicles. The snowmobile perhaps more than any other off-road vehicle presents the greatest threat because it provides supreme mobility at a time when the rest of nature is least mobile (Ives 1974). Harassment of ptarmigan may be an important issue with use of snowmobiles in wintering areas. Flushing of birds may increase their vulnerability to predation, force them to expend energy, or temporary displace them from optimal feeding, roosting, and/or loafing sites. Compaction of snow and running over willows are also potential negative impacts of snowmobiling with direct consequences to ptarmigan.

Twenty-five major ski resorts occur within Colorado (24) and southern Wyoming (1) of which at least 18 access terrain at or above treeline. The highest approved lift reaches 3,915 m, but skiers can hike to elevations over 3,963 m at some resorts. Twenty-three of the ski areas are on lands administered by the USFS, including all 18 of the areas that extend to treeline and above. Ptarmigan are still present in these areas, but Braun et al. (1976) suggested that numbers may be less than before development. Detrimental impacts of skiers (disturbance) and ski area development (loss of habitat) on white-tailed ptarmigan are poorly documented. However, some ptarmigan likely are displaced from suitable habitats by the activity associated with ski areas. Others are continually disturbed and forced to expend energy needed for feeding and staying warm. Furthermore, activities at ski areas are no longer limited to the winter period. Numerous resorts now cater to summer recreationists, providing access to the alpine via ski lifts and trails throughout the summer.

Besides the disturbance factor, direct habitat loss and degradation may occur at ski areas. For instance, willows on ski runs may impede skiers, and where they extend above the snow surface, they are likely to be removed or cut. Habitat loss also may take place due to snow-making operations that prematurely cover willows that would otherwise be exposed. In places where willows are left standing, they may be repeatedly run over and damaged by skiers or machines used to groom ski trails. In addition, these same activities compact the snow and may force ptarmigan to move longer distances to find suitable snow for roosting. Developments associated with ski areas often contribute to further loss and degradation of willow stands along stream courses below treeline. These stands may be extremely important habitat during severe winters when snow covers willow at the higher elevations.

Power poles and lifts extending above treeline serve as perching sites for raptors and corvids. Ptarmigan also may be killed by flying into wires and cables attached to the poles and lift towers (Storch 2000). Probably the most pronounced effect of ski area development based on studies of rock ptarmigan in Scotland (Watson and Moss 2004) is the influx of generalist predators, such as common ravens and foxes. Following development, rock ptarmigan breeding success declined on areas up to 4 km from the center of development due to nest predation by crows and possibly gulls (Watson and Moss 2004). On the area nearest the development, densities declined to where no breeding pairs were detected for 17 consecutive springs.

Mining

Mining has been an important industry within the range of the white-tailed ptarmigan since the 1860's. Historically, mining was far more widespread, but on a much smaller scale than at present. Although individual mines were often smaller than today's mines, they tended to be clustered into large, densely populated mining districts, such as those at Leadville, Cripple Creek, Silverton, and Central City. In the absence of any environmental regulations, the combined impacts of the many mines comprising the mining districts and the accompanying processing and support facilities were devastating. Most operations were simply abandoned when the gold and silver deposits were depleted. Nearly 150 years later, the negative consequences still persist and may never be completely rectified (Larison et al. 2000, Larison 2001).

Brown et al. (1978b) estimated that 34,677 ha of alpine have been disturbed by mining in the western United States, excluding Alaska. This represents about 1 percent of the total area of alpine and 10 percent of the total area (343,805 ha) that has been disturbed (Brown et al. 1978b). Within the occupied range of ptarmigan in Region 2, mining has disturbed approximately 2,177 ha (0.3 percent) of land above 3,292 m elevation.

The impacts of modern mining operations result not only from the surface disturbing activities of mining, but also the construction of roads, power lines, buildings, and other ancillary facilities. Other associated impacts include excessive dust from the operation of large equipment, spillage of petroleum products, and disruption of surface and ground water flows (Brown et al. 1978b, Chambers 1997, Macyk 2000). Mining operations in certain geologic formations also can result in the release of acidifying and metal-laden effluents into surface and subsurface waters. In addition, mining on steep slopes increases the probability of mass slumping. Mining is by far the most disruptive of man's activities in the alpine (Brown et al. 1978b, Chambers 1997, Macyk 2000). Disturbances associated with mining result in the nearly complete destruction of alpine soils and vegetation. Today, implementation of stricter environmental regulations and improved mining and reclamation practices has reduced the impacts of mining. However, reclamation of disturbed lands in alpine regions represents a unique challenge due to severe climate and limited soil resources. Although significant progress has been made in reclaiming alpine sites (Brown et al. 1978a, Brown et al. 1978b, Brown and Johnston 1979, Chambers 1997, Macyk 2000), the knowledge base is far less than what is known about reclaiming disturbed lands in other life zones. Of greatest concern is the lack of long-term data on the success of reclamation efforts in the alpine. Numerous techniques have been developed to neutralize some of the impacts associated with mining, but they are expensive, require continued monitoring and maintenance, are impractical on poorly accessible sites, and most importantly, they are designed to treat the symptoms of the problems and not fix the problems themselves (Brown et al. 1978b).

Global climate change

One of the greatest potential threats to ptarmigan and the alpine ecosystem upon which they depend is global climatic change (Walther et al. 2002, Wang et al. 2002a,b, Krajick 2004). Global average temperatures have increased by 0.6 °C in the past 100 years, with the greatest rate of increase occurring since 1976 (Walther et al. 2002). Climate models predict that warming will accelerate in the first half of the 21st century; the uncertainty is how much of an increase will take place (Billings 1995). Some models predict that global mean air temperatures could be 2 to 4 °C warmer by 2050 (Billings 1995). Using weather data collected at Niwot Ridge along Colorado's Front Range, Wang et al. (2002b) predicted minimum winter temperatures will increase 2.3 °C (Canadian Climate Center model) and 2.6 °C (Hadley Centre model) by 2030. Their models also predicted more variable weather conditions and greater frequency of extreme events.

Whereas ptarmigan are well-adapted to coping with cold temperatures, they are ill-adapted to dealing with high temperatures (Johnson 1968, Martin et al. 1993, Martin and Wiebe 2004). The main consequences of climate change to ptarmigan are the loss and fragmentation of habitat through (1) changes in the quality and quantity of snow cover, (2) changes in the distribution and composition of plant communities, and (3) upward movement of treeline. As treeline rises, alpine areas will become smaller and less continuous. Opportunities for migration, emigration, and immigration will decrease. Populations of ptarmigan will become increasingly isolated and more vulnerable to extinction by extreme, stochastic events, which models already have predicted will increase in frequency. Demographic rescue is a critical feature of white-tailed ptarmigan populations; without the prospect for regional immigration, it is unlikely that population viability can be maintained (Martin et al. 2000, Sandercock et al. 2005a).

Wang et al. (2002b) suggested that warmer winter temperatures may be partially responsible for the long-term decline of white-tailed ptarmigan in Rocky Mountain National Park. Warmer spring temperatures have been correlated with earlier egg laying in white-tailed ptarmigan, but this has not been found to affect the population growth rate (Wang et al. 2002b). On average, median hatch dates have advanced 15 days over the past 25 years in Rocky Mountain National Park (Wang et al. 2002b).

The precise impacts of warmer temperatures on snowpack in the alpine are uncertain. Warmer temperatures could lead to more violent and frequent storms and therefore increase the snowpack. Conversely, warmer temperatures could truncate the period when snow falls and increase melting, thus, reducing the snowpack. Regardless, the ecology and habitat use patterns of white-tailed ptarmigan could be greatly impacted by any long-term changes in snowfall patterns. Snowfall patterns in combination with topography and wind ultimately govern the distribution, composition, and structure of alpine plant communities (Billings 1988). Thus, any long-term changes in snowfall patterns will eventually alter these features, presumably to the detriment of ptarmigan. For example, wet meadows below late-lying snowfields are one of the most productive of all alpine plant communities and are vital brood-rearing and summer use areas for white-tailed ptarmigan (Braun 1971a). These areas will shrink or disappear if warmer winter temperatures equate to less snowfall.

The selection of nest sites and length and timing of incubation breaks may be constrained by ambient temperatures (Wiebe and Martin 1997, 1998b). Embryos are generally more tolerant of cold temperatures than even short exposures to temperatures above 40 °C (Webb 1987). Rising temperatures may force ptarmigan to nest in denser vegetation where they may be more vulnerable to predation. They also may take fewer incubation breaks, especially during the day when temperatures are highest. If nesting hens cannot obtain sufficient food, their body condition will deteriorate and they may abandon the nest.

Carbon dioxide is the main and most abundant "greenhouse" gas contributing to global warming. Aside from the effects of increasing temperatures on alpine plant communities, there are the additional direct effects of increasing carbon dioxide levels in the atmosphere on photosynthesis and growth of alpine plants. Alpine plants, because of their greater photosynthetic efficiency at low carbon dioxide concentrations, may actually benefit from exposure to a carbon dioxide-enriched atmosphere (Korner and Diemer 1994). However, the long-term consequences of this exposure and the resultant change in the composition and structure of plant communities remain unknown. Together, the combine effects of increased carbon dioxide levels and nitrogen deposition may significantly alter alpine plant communities with unknown consequences.

Pollution

Environmental conditions in the alpine have selected for plants with low growth rates, small stature, high resource allocation to below ground organs, and slow rates of resource capture. Many of the dominant species respond slowly to changes in resource supply. Conversely, some of the rarer, ruderal species respond more quickly to enhanced resource availability. Thus, any environmental perturbation in the alpine that increases the supply of soil nutrients bolsters the success of the ruderal species, potentially at the expense of the dominant species (Theodose and Bowman 1997).

The Front Range of the southern Rocky Mountains has experienced significant increases in atmospheric nitrogen deposition over the past several decades due to increased agricultural, industrial, and suburban development (reviewed by Bowman et al. 2004). Although rates of nitrogen deposition are low compared to the northeastern United States and Europe, the high elevation alpine systems of the Rocky Mountains are more susceptible to ecological change. Thus, it takes lower amounts of nitrogen before alpine systems may begin to experience adverse environmental conditions. There is compelling evidence that nitrogen deposition has caused significant biotic changes in alpine aquatic ecosystems (Baron et al. 2000). For terrestrial alpine systems, long-term vegetation records indicate that plant species composition is changing in a manner consistent with a nitrogen fertilization effect, but results are not conclusive (Bowman et al. 2004). Because nearly 50 percent of nitrogen deposition is entrapped in snow and snow is not evenly distributed across the alpine, the potential for change in plant species composition is greatest in communities with the most snow cover. These are the same communities used by ptarmigan. Any major changes in alpine plant communities, regardless of the cause, must be considered a threat to ptarmigan populations.

Alpine areas have always been subject to strong fluxes of incoming solar ultraviolet radiation due to the thinner atmosphere at high elevations. However, the 20th century has experienced increases in UV-B irradiation due to the breakdown of the stratospheric ozone screen caused by the release of man-made chlorofluorocarbon gases (Molina and Rowland 1974, Rowland 1989, Billings 1995). Caldwell et al. (1982) found that UV-B radiation inhibits photosynthesis. Alpine plants have evolved and adapted accordingly to naturally high UV-B levels and reflect or screen it out epidermally. However, it is uncertain what will happen to the ecophysiology of alpine plants if UV-B levels continue to increase (Billings 1995).

Cadmium is ubiquitous in natural environments. It also is extremely toxic and can be readily mobilized by certain human activities, such as mining; therefore, it is considered a potential health threat to wildlife (Scheuhammer 1987, Larison et al. 2000). Cadmium in runoff of mine sites is often deposited downstream in wetlands where it can accumulate and be absorbed and biomagnified by willow, the single most important food item for white-tailed ptarmigan (Larison et al. 2000). Cadmium poisoning causes renal failure, which in turn affects calcium balance and skeletal integrity. Because females winter at lower elevations than males, they are at greater risk of exposure to higher concentrations of cadmium in their diet. Females also are more susceptible to cadmium poisoning due to their greater demand for calcium during egg-laying. Consequently, owing to the age-dependent accumulation of this toxic metal, mortality is highest in adults, and especially adult females (Larison et al. 2000). Increased mortality of older females can have a pronounced effect on the population because they are the most productive individuals (Sandercock et al. 2005a). Larison et al. (2000) reported that contaminated populations had highly skewed sex ratios (3:7) favoring males, and these habitats supported fewer breeding ptarmigan than found in other populations.

The extent to which cadmium affects ptarmigan populations in Region 2 is uncertain. The only location where cadmium poisoning has been shown to impact skeletal integrity, reproductive performance, and survival of ptarmigan is in the Upper Animas River Watershed in southwestern Colorado (Larison 2001). However, Larison (2001) detected elevated cadmium levels in kidney tissues from ptarmigan collected throughout the Colorado ore belt. Based on this finding, Larison (2001) postulated the cadmium problem may extend beyond the Animas River Watershed to other areas within the ore belt and might even extend to populations outside the ore belt. Intensive studies of ptarmigan elsewhere in Colorado provide little support for this theory. There has been no apparent evidence (i.e., skeletal abnormalities, skewed sex ratios favoring males, and unusually high mortality of adult females) of cadmium poisoning in ptarmigan populations studied at Crown Point, Niwot Ridge, Mt. Evans, Rocky Mountain National Park, Guanella Pass, Independence Pass, and Mesa Seco (Braun 1969, Braun and Rogers 1971, May 1975, Martin et al. 2000, Sandercock et al. 2005a).

Higher than expected concentrations of semi-volatile organochlorine compounds have been detected in snow samples at high altitudes in western Canada (Blais et al. 1998). This is the result of a process known as cold condensation – the progressive volatilization of these compounds in relatively warm locations (i.e., near their source in industrial and agricultural centers), the long-range transport of the compounds in the atmosphere, and their subsequent deposition at enhanced concentrations in cooler environments (higher altitudes) in the form of snow. Alpine areas in the Southern Rocky Mountains may be particularly susceptible to this process because they tend to receive high levels of precipitation while being close to much warmer, low elevation, pollutant sources (Blais et al. 1998). The toxicity to wildlife resulting from direct exposure to these chemicals has been intensively studied (Hudson et al. 1984), but the effects on wildlife living at high elevations from indirect exposure via cold condensation remain unknown.

Hunting

Within the United States, white-tailed ptarmigan are legally hunted in Alaska, Colorado, Utah, and California. Ptarmigan are unwary and easily approached by humans. In the fall, they concentrate in large flocks on traditional use areas. Even when repeatedly disturbed, they continue to use the same areas. These traits make them exceptionally vulnerable to over-harvest. This is especially true for easily accessible populations that occur along Colorado's Front Range within 1 to 2 hours driving distance of major cities.

Braun (1969) estimated that hunting of white-tailed ptarmigan on two study areas increased their annual mortality rate by 15 and 27 percent. He suggested that hunting on one of the areas was not entirely replacive and was instead partially additive and likely depressed population densities on this area. Smith and Willebrand (1999) similarly concluded that hunting of willow ptarmigan was primarily, if not totally, additive to natural mortality. Other grouse investigators have reached the same conclusion (Ellison 1991, Small et al. 1991, Steen and Erikstad 1996). If hunting is additive, the effects should result in a declining breeding population. However, this may not always be the case. Immigration from non-hunted or lightly hunted populations may sustain densities on some heavily hunted areas (Small et al. 1991, Smith and Willebrand 1999). Thus, the effects of hunting may go undetected, or hunting may be interpreted as having no effect because breeding densities remain stable.

In some populations, female greater sage-grouse (*Centrocercus urophasianus*) have higher hunting mortality than adult males (Connelly et al. 2000). In this study, adult females were believed to be more susceptible to hunting mortality because of their association with broods and their brood behavior in the fall. Males tended to be more widely dispersed and difficult to locate. This scenario may or may not apply to ptarmigan depending on location. Braun and Rogers (1971) found that during the hunting season males and unsuccessful females at Mt. Evans and Independence Pass associated in large flocks and, once located, were easily harvested. Hens with broods were scattered and less likely to be found by hunters. In contrast, males and unsuccessful females at Crown Point were in small flocks in rocky areas that were not searched by hunters. Brood habitat was limited and occurred along the edges of the rocky areas. As a result, hens with broods were more easily located by hunters and comprised the bulk of the harvest at Crown Point each year (Braun and Rogers 1971). In areas such as Crown Point, where the susceptibility to hunting of successful hens, especially older hens, is greater, the overall productivity of the population may decline (Sandercock et al. 2005a).

Currently, the threat of over-harvest of white-tailed ptarmigan is limited to localized areas. However, this threat may become more wide-spread and pronounced as Colorado's human population grows. This, combined with the proliferation of 4-wheel drive vehicles and 4-wheel drive roads in Colorado that lead to or traverse alpine areas, makes access to ptarmigan populations relatively easy for more people. As opportunities diminish for hunting other declining grouse species, an increasing number of hunters are expressing interest in hunting ptarmigan. Another feature that attracts interest in hunting ptarmigan is the fact that over 90 percent of the occupied habitat in Colorado is publicly owned and open to hunting.

Water developments

Alpine ecosystems are vitally important as metropolitan, industrial, and agricultural watersheds, providing nearly year-round snow accumulation and water storage (Johnston and Brown 1979). Alpine systems have been subject to experimental augmentation and manipulation of the snowpack in efforts to enhance water supplies (Martinelli 1966, Steinhoff and Ives 1976, Johnston and Brown 1979). Any attempt to artificially increase the snowpack in alpine areas will significantly affect plant processes in several ways. Most importantly, it will shorten the growing season. Depending on the length of the delay of snow melt, plant production and reproductive success will be correspondingly reduced. Composition and structure of plant communities could be drastically altered due to increased moisture. The most deleterious and direct effect on ptarmigan would be a reduction in the availability of willow. Traditional wintering and breeding areas may be abandoned due to excessive snow cover. Birds would be forced to move to lower elevations below treeline to find willow. This may expose them to predators that are usually absent above treeline in the winter. In the spring, breeding activities would be delayed because bare areas for nesting would not become available until later in the season. Even then, fewer areas would be available for nesting.

The growing demand for water has prompted the need to construct more and larger reservoirs and to expand existing reservoirs to capture and store water until it is needed. These reservoirs have been constructed at all elevations. Invariably, reservoirs constructed in the subalpine and alpine eliminate large expanses of willow to the detriment of ptarmigan (Braun et al. 1976). Roads leading to these reservoirs typically follow stream courses, resulting in the further loss of willow. The effects on ptarmigan may be compounded if the reservoirs are open to the public and result in increased recreational activity in the area.

Management Activities of White-tailed Ptarmigan in Region 2

Implications and potential conservation elements

Immediate activities affecting white-tailed ptarmigan populations in Region 2 are grazing, recreation, mining, and water developments. Historically, unregulated and widespread grazing of alpine areas posed the greatest threat to ptarmigan populations in Region 2. Over the last four to five decades, there has been a gradual reduction in domestic livestock use of alpine areas. Thus, the negative consequences of this activity have become more localized and less of a threat to the long-term stability of ptarmigan populations in Region 2. Even so, about 28 percent of the alpine lands managed by the USFS in Region 2 are currently permitted for grazing by domestic livestock (**Figure 5**). Another 19 percent are open to grazing but currently vacant (**Figure 5**), including 91 percent of the occupied range of white-tailed ptarmigan in Wyoming. The proportions of alpine lands permitted for grazing in each forest are as follows: Arapaho-Roosevelt (1 percent), White River (14 percent), Pike-San Isabel (14 percent), Routt-Medicine Bow (30 percent), San Juan (33 percent), Rio Grande (49 percent), and Grand Mesa-Gunnison-Uncompahgre (61 percent) (**Figure 6**). Approximately 75 percent of alpine range that is actively grazed in Region 2 occur in southwestern Colorado within the Grand Mesa-Gunnison-Uncompahgre, San Juan, and Rio Grande national forests (**Figure 5** and **Figure 6**).

For other species of upland birds, the primary issue with grazing is its profound effect on the availability of residual cover required for nesting. For

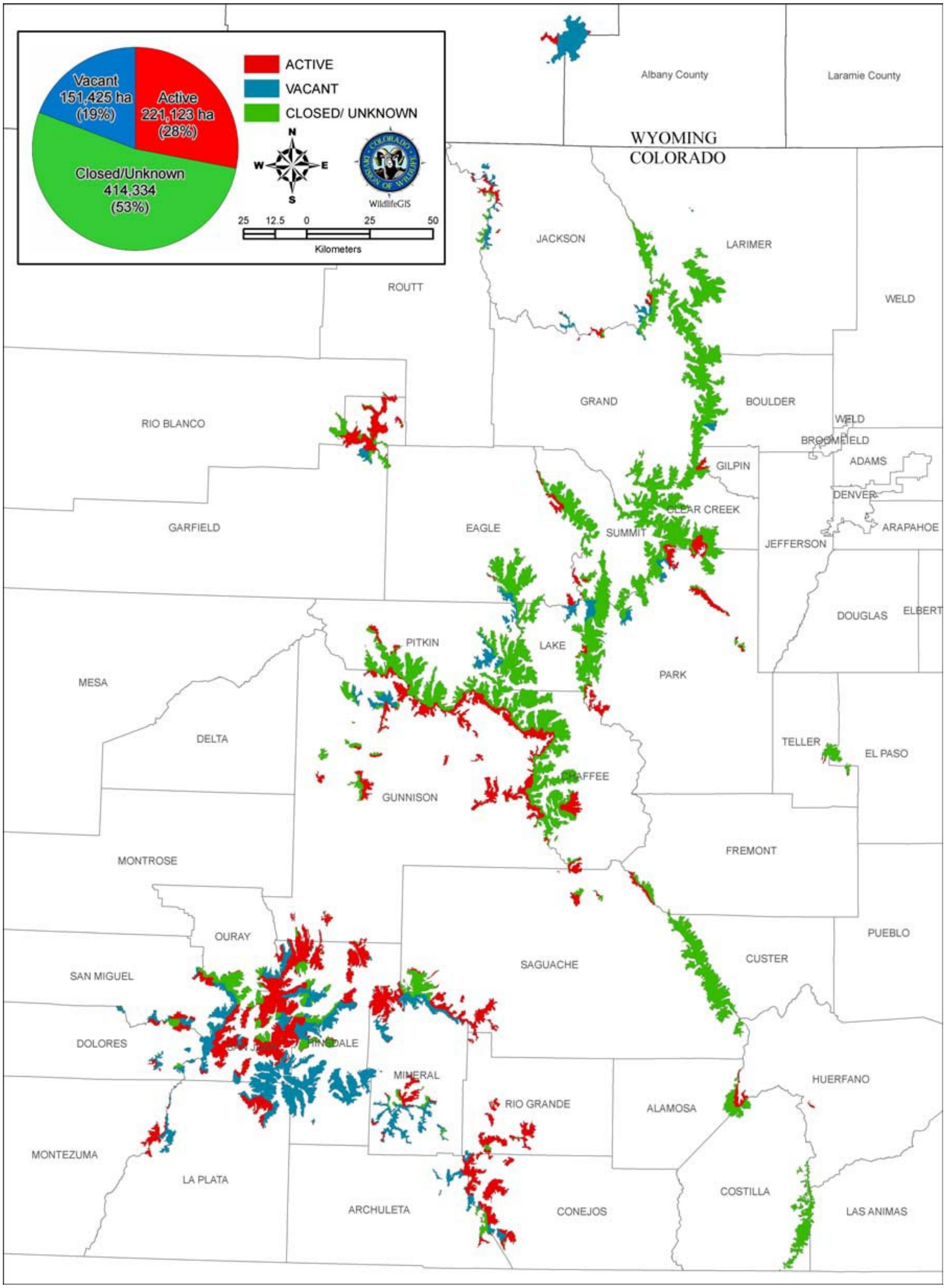

Figure 5. Grazing status (active, vacant, or closed) of alpine ranges within the Rocky Mountain Region (Region 2) of USDA Forest Service.

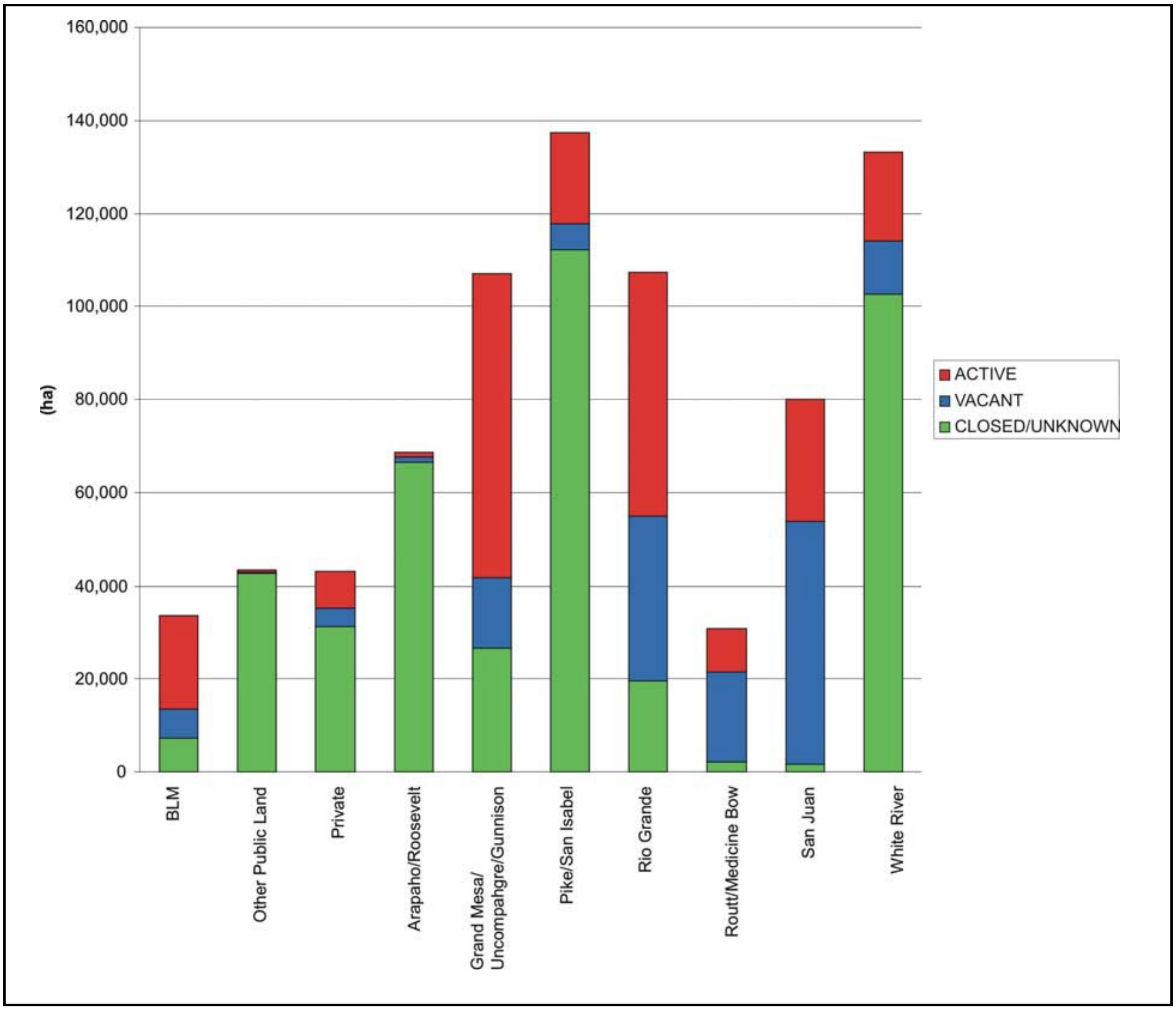

Figure 6. Distribution of grazing activity by land ownership on alpine ranges within the Rocky Mountain Region (Region 2) of the USDA Forest Service.

ptarmigan, however, the primary issue pertains to food availability. Some plants heavily used by domestic sheep are also important foods for ptarmigan. Sheep are released on the alpine in July during or shortly after the peak of ptarmigan hatch. Although newly hatched chicks are mainly consuming insects, they quickly shift their diet to plant matter similar to adult ptarmigan (May 1975). Consequently, sheep are in direct competition with all age and gender classes of ptarmigan for food. This competition may be especially critical for young birds because it occurs at a time when certain foods are necessary to insure proper growth. Having the option to alter grazing patterns from year to year would reduce some of the competition. However, due to the short growing season and the difficulty in accessing alpine ranges, grazing during the growing season is the only option. Given this scenario, a strong argument can be made that alpine ranges are ecologically unsuited for grazing by domestic livestock.

In contrast to grazing, recreational activities in the alpine have increased during all seasons of the year. USFS Chief Dale N. Bosworth names unmanaged recreation as one of the four major threats to the health of the nation's forests and grasslands (www.fed.fs.us/projects/four-threats). There is no evidence to suggest that present levels of recreation are affecting ptarmigan populations in Region 2, except possibly in local areas. Of concern, however, is that the level of activity will continue to increase, and that conflicts between recreationists and wildlife will escalate in Region 2. The notion that recreation is a benign activity with regards to wildlife because it is spread over large areas and takes place in many different forms is no longer tenable. The many types of recreational activities are in themselves a problem. Managers are faced with the daunting task of trying to reliably evaluate the cumulative effects of all the different ways people recreate. It is much easier to focus on one group as evidenced by the recent proposed regulations to govern off-road vehicle use on national forests and grasslands (USDA Forest Service 2004). By themselves, recreational activities such as skiing, hiking, and off-road vehicle use may cause minimal or only localized conflicts with wildlife, but their combined impact may result in significant disturbance or habitat degradation. Managing one form of recreation to minimize conflicts with wildlife without simultaneously considering the other types of recreation occurring in the area may not solve the problem.

It is predicted that people with more expendable income and leisure time will continue to move into Region 2 and will be looking for new and different places and ways to recreate. Alpine areas are likely to be particularly attractive to this growing sector of the population because of the preponderance (over 90 percent) of lands under public ownership. Alpine areas already have become a popular destination for ecotourism, a form of organized recreation that focuses on bringing tourists to biologically rich and unique ecosystems. This form of recreation will also undoubtedly continue to increase.

An example of an area under heavy and multiple types of recreational use that could potentially impact ptarmigan is Guanella Pass, the largest known wintering area for white-tailed ptarmigan in Colorado (Braun et al. 1976). About a one-hour drive west of Denver, this site has become one of the most popular destinations in the world for viewing and photographing white-tailed ptarmigan. Besides the viewers and photographers, hikers, back-country skiers, and snowshoers also are frequent users of the Guanella Pass area (Schenk and Powers 2006). Several trails start at the top of the pass, including the trail to Mt. Bierstadt, one of Colorado's easiest and most accessible 14,000 ft. (4,267 m) peaks to climb during winter. This trail bisects the entire ptarmigan wintering area. The popularity of the Guanella Pass area has resulted in the U.S. Department of Transportation, Federal Highway Administration designating the road a scenic byway. Construction is underway to upgrade the road and to build a parking lot at the top of the pass, which will improve access to the pass and attract more visitors to this sensitive area (Schenk and Powers 2006).

Mining is probably the most destructive activity occurring in the alpine. Fortunately, its effects are not currently widespread, but there is the constant threat that mining activities may expand in the alpine as the industry develops new, more efficient ways to find and extract resources. Alpine ranges have virtually no chance of recovering from the effects of mining. Furthermore, despite major advances in alpine restoration techniques, the mining industry does not have the ability to restore disturbed areas to pre-mining conditions. It is uncertain whether restoration techniques currently being applied are even adequate to establish plant communities that will eventually be occupied by ptarmigan. Just restoring plant communities may not be enough to insure that ptarmigan will reoccupy the site without attention to other details of the landscape, such as the distribution and amount of rock cover.

Based on the estimated water demand in 2000, future municipal and industrial water needs in Colorado are predicted to increase 53 percent (630,000 acre feet) by 2030 from 1,194,900 acre feet to 1,824,900 acre feet (Colorado Water Conservation Board 2004). Options for meeting the demand primarily involve better conservation and expansion of existing storage facilities. However, the Colorado statewide water supply initiative clearly acknowledges that few municipal and industrial water providers have identified supplies beyond 2030; thus, more aggressive solutions may be necessary to meet the demand beyond 2030 (Colorado Water Conservation Board 2004). Construction of new storage facilities and augmentation and manipulation of the snowpack are two potential solutions, both of which may have serious negative consequences to ptarmigan (Braun 1971a, Braun et al. 1976).

Global warming is a highly contentious and politically sensitive issue that extends far beyond the bounds of Region 2 and the scope of this assessment. It is mentioned in this assessment only to raise awareness that plants and animals found almost exclusively in the alpine may be the first to decline or become extinct as a result of changes in global climate. In terms of white-tailed ptarmigan, global climate change has the potential of having consequences on a larger scale than the combined effects of grazing, recreation, mining, and water developments. Consequently, global warming must be recognized as one of the most serious threats to the long-term persistence of white-tailed ptarmigan populations in Region 2 and throughout the species' range in western North America. The critical issue is no longer if global warming is occurring, but rather how to stop and eventually reverse its effects on wildlife and wildlife habitats. Climate research throughout the world has confirmed that global warming will likely continue for decades to come even if steps are taken now to address the problem.

Tools and practices

Inventory and monitoring populations

Presently, the only reliable technique for censusing white-tailed ptarmigan involves play-back of tape-recorded male challenge calls (Braun et al. 1973). The primary drawback of this technique is that it can only be applied to small areas ($\leq 2\ km^2$) without an intensive effort by many individuals. There are no known methods for accurately estimating white-tailed ptarmigan densities over broad geographic areas. Aerial surveys used to census willow ptarmigan in southwestern Yukon, Canada (Pelletier and Krebs 1998) are neither practical nor safe to fly in alpine areas typical of Region 2. Line-transect sampling, although proven reliable for estimating breeding densities of male willow ptarmigan in Canada (Pelletier and Krebs 1997), cannot be accurately or efficiently applied to estimate densities of white-tailed ptarmigan. The reasons being: (1) white-tailed ptarmigan naturally occur at low densities, (2) their secretive nature makes them difficult to detect, and (3) they live in rugged terrain that is difficult to access during the breeding season Therefore, tremendous effort would be necessary to meet the minimum sample size (60 to 80 observations) requirements of the line-transect method for calculating $f(0)$ (Buckland et al. 1993).

Despite its limitations of being labor intensive and only suited for small areas, the play-back technique is exceptionally effective in locating territorial males. In a series of weekly tests from 10 May to 20 June on two small areas in Rocky Mountain National Park, Braun et al. (1973) located all known territorial males when the technique was used prior to 1000 hours. About 90 to 95 percent of the territorial males responded when the call was used after 1600 hours. During these late-day surveys, Braun et al. (1973) found that response rates progressively increased as dusk approached. Braun et al. (1973) also found that males responded anytime of day during periods of foggy or snowy weather, but it was more difficult to determine their exact location under these conditions.

On calm days, males may be heard calling from over 500 m away. The response of one male often initiates a chain reaction of responses from nearby males. Males within 100 m when the call is first played are most likely to respond back with their own challenge call. Males farther away may respond by performing a flight scream (Schmidt 1988). During the flight scream, the male calls while flying to a prominent location within his territory. He often continues calling once he lands. He may repeat this performance several times as he flies around the boundary of his territory searching for any intruding males. If the male has a mate, he usually returns to her within several minutes. It is best not to play the call again while the male is flying around his territory because it will only delay his return to his mate. Wait quietly and watch until he returns to the area where he first responded to the call. Approach the area and try to locate the male. If unsuccessful in finding the male, play the call briefly and he should respond without flying. Generally, if he has a mate, she will be sitting within 2 to 3 m. Unmated males are more likely to run when approached. Mated males will be reluctant to leave the area. Non-territorial males may or may not respond to the call. At times they respond only once; other times they may fly away to avoid a possible confrontation with a territorial male.

The play-back of taped-recorded calls can be used to quickly assess the presence or absence of breeding ptarmigan in an area. More precise monitoring requires repeated (two to four) visits to an area to insure that all the territorial males are located. The technique is designed to produce an exact count of mated and unmated territorial males within a given area. Non-territorial males may be missed.

The inaccessibility of most alpine areas coupled with the rugged terrain, soft snow, and poor weather conditions add to the difficultly of conducting counts during the spring breeding season. Road transects are not an option due to the lack of roads and the fact that most roads in the alpine are not passable until early June or later. The only feasible way to conduct the count is on foot, which limits the size of the area that can be effectively searched. Counts are obtained by walking all snow-free areas adjacent to patches of willow within the area to be surveyed and playing the call every 150 to 200 m while listening for a response.

Females with broods can be located using chick distress calls (Braun et al. 1973). The calls work best for females with chicks under 3 weeks of age, but females accompanied by chicks up to 7 weeks of age will respond. Females respond by clucking, jumping up on a boulder, or running towards the source of the call. They may even attack the person playing the call. The intensity of the female's response depends on the age of the chicks. Females with older chicks may only respond with a few light clucks and exhibit no aggressive behavior. Use of the chick distress call enabled Braun et al. (1973) to locate all (*n* = 12) females successfully hatching their clutches whose nests they had under observation.

Use of the chick distress call has limited application as a method for assessing productivity because it is more effective in locating females with chicks than those without chicks. Thus, for management purposes, the call is only useful in determining the number of females with chicks and average brood size within the area searched. It can only be used to estimate nesting success on intensively studied areas where females are captured and marked during the breeding season and subsequently located during the brood-rearing season. This type of intense monitoring is impractical for management purposes.

At times, the play-back of chick distress calls can elicit a response from birds (males and females without chicks) in flocks. They may call, become more vigilant, and/or move in response to the call, all of which makes them easier to detect. The only other way to find flocks of males and broodless females is by intensively searching potential summer habitat. In this case, they can be easily missed by inexperienced observers.

Another option for assessing productivity is by examining wings from hunter-harvested birds. Wings are collected at hunter check stations or through the operation of volunteer wing collection stations placed at strategic access points to popular hunting areas (Hoffman 1981). Most grouse species, including ptarmigan (Braun and Rogers 1967), can be classified to age and gender based on the examination of wing characteristics. Therefore, wing samples reveal information about the autumn structure of grouse populations (Hoffman 1985). Two useful indices of productivity obtained from wing samples are the percent juveniles in the harvest and the ratio of juveniles to females (Hoffman 1985). It also is possible to obtain a crude estimate of nesting success from wing samples and to estimate hatching dates (Giesen and Braun 1979a, Hoffman 1985).

The validity of using information obtained from wing samples to draw conclusions about the population is based on the assumption that different age and gender classes are harvested in proportion to their occurrence in the population. This assumption is probably valid for white-tailed ptarmigan. When the season opens in mid-September, females with chicks are using the same general areas as the males and broodless females. Hunters therefore have an equal chance of encountering all age and gender classes. At current hunter densities and harvest levels, the major challenge is obtaining adequate and representative samples of wings from locations throughout Region 2.

Inventory and monitoring habitats

As recommended by Connelly et al. (2003) for greater sage-grouse, habitat characterization for white-tailed ptarmigan should follow the processes described by Johnson (1980). Johnson (1980) described habitat selection as a hierarchical process and used different levels of selection to illustrate this process. First-order selection represents habitat characteristics within the geographic range, second-order selection represents habitat characteristics of the home range, third-order selection represents the use of different habitat components within the home range, and fourth-order selection represents habitat characteristics of particular use sites (i.e., feeding, loafing, escape, nesting, brood-rearing). The orders range from macro- to micro-scale components for habitat selection. Analysis of habitat use at both scales is important for understanding animal-habitat relationships (Litvaitis et al. 1994). For white-tailed ptarmigan, macro-scale habitat components (first and second order selection) of seasonal use areas are more clearly described and understood than micro-scale habitat components.

Features of the landscape important in delineating breeding areas are the presence of willow and snow-free areas. Critical components of brood-rearing and summer use sites are rocky areas for cover and lush herbaceous vegetation for food. For wintering areas, the essential elements are the presence of willow above the snow for food and soft snow for roosting. At the Regional scale, these important habitat features can be quantified using Geographic Information Systems (GIS) techniques. Mapping of the distribution of willow in subalpine and alpine zones will provide valuable information in identifying potentially suitable habitats for white-tailed ptarmigan, especially if high resolution aerial photographs and satellite imagery are available from all seasons of the year. For example, examination of photographs and imagery taken during early March and early May would be extremely beneficial in identifying potential wintering and breeding areas, respectively. Likewise, mapping of late-lying snow fields adjacent to herbaceous meadows and rocky areas using photographs and imagery taken during August and early September would be a starting point for identifying potential brood-rearing and summering areas, respectively. Aerial photographs and satellite imagery in combination with

GIS technology also can be used to ascertain the size of habitat patches, juxtaposition of habitat patches, and distance between habitat patches. Establishment of baseline information is necessary for subsequent monitoring of long-term trends in habitat availability and for evaluating the effects of land use changes and management actions.

The next level of habitat monitoring (micro-scale) is to measure features of the habitat where white-tailed ptarmigan occur. At this level, emphasis should be placed on measuring habitat variables that are of potential biological importance to ptarmigan (**Table 9**). For these data to be meaningful, an unbiased characterization of the habitat is necessary. This involves measuring habitat attributes at ptarmigan use sites as well as at random sites using the same techniques. Where appropriate, stratification, such as by use (grazed, ungrazed) or density of ptarmigan (high, medium, and low), will provide more meaningful information The most applicable methods for measuring micro-habitat characteristics in alpine areas are the line intercept (Canfield 1941) and Daubenmire plots (Daubenmire 1959) or variations thereof. The line intercept method is best suited for estimating shrub cover while Daubenmire plots have advantages in estimating herbaceous cover. The two methods can be used in conjunction with each other. Regardless of the method used, cover values should be recorded by species rather than by categories of species (i.e., grasses, forbs, shrubs).

Frederick and Gutierrez (1992) measured habitat variables in 0.02-ha circular plots at sites used and unused by white-tailed ptarmigan in the Sierra Nevada. Cover values were measured along two 15-m line intercepts that crossed in the plot center. Melcher (1992) used a combination of line transects and 1-m^2 quadrants to measure willow characteristics at sites used by white-tailed ptarmigan in relation to browsing by elk. Few other studies of white-tailed ptarmigan have attempted to quantitatively measure habitat attributes at the micro-scale. Most published habitat information on white-tailed ptarmigan is descriptive in nature. Consequently, standardized techniques for measuring micro-scale characteristics of habitats used by white-tailed ptarmigan are not well established. Standardized techniques are necessary to provide rigorous and consistent data sets to allow for valid comparisons among areas and years (see Connelly et al. 2003 for greater sage-grouse example).

Management approaches

Management tools, such as the use of fire, grazing, mowing, and spraying, designed to maintain, enhance, or restore plant communities in other life zones are rarely, if ever, applicable in the alpine. The natural processes that perpetuate alpine ecosystems are still intact. Human intervention is not necessary other than to insure that these natural processes are not disrupted. The key to the successful management of alpine

Table 9. Habitat variables of potential importance to white-tailed ptarmigan.

Habitat variable	Season of Importance
Distance to willow cover	Winter, spring, and fall
Frequency of occurrence, density, and percent cover of willow	Winter, spring, and fall
Minimum, maximum, and mean willow height	Winter, spring, and fall
Willow patch size and configuration	Winter, spring, and fall
Distance to rock cover	Spring, summer, and fall
Frequency of occurrence, density, and percent cover of rocks	Spring, summer, and fall
Minimum, maximum, and mean rock diameter	Spring, summer, and fall
Rock patch size and configuration	Spring, summer, and fall
Frequency of occurrence, density, and percent forb cover	Summer and fall
Frequency of occurrence, density, and percent cover of graminoids	Summer and fall
Distance to snow	All seasons
Percent snow cover	Winter and spring
Percent bare ground	Winter and spring
Distance to nearest other vegetation type	All seasons
Species richness	Summer and fall

ecosystems is protection – protection against over-use due to grazing, recreation, mining, and development, and protection from environmental perturbations that contribute to global warming, deposition of nitrogen and toxic compounds, and depletion of the ozone layer. In spite of technological advances in restoration techniques, there is little that can be effectively done over large areas once alpine areas become seriously degraded. Proactive protection is the only solution. Factors that impact alpine ecosystems cannot be allowed to reach the point where fixing them becomes difficult or impossible, or requires decades if not centuries of protection to correct. Even then, there is no guarantee the system will restore itself.

Management efforts must focus on developing regulations that allow only light to moderate use of alpine areas. Ample resources must be allocated to enforce regulations and to levy strong penalties when the regulations are violated. Management strategies must not only include the regulatory component for allowable activities but also the regulatory component for excluding certain uses that are inappropriate or incompatible with maintaining healthy alpine communities. The management philosophy needs to be one of reasonable, sustainable use rather than multiple use.

The same principals that apply to management of ptarmigan habitats also apply to management of ptarmigan populations. Little if any human intervention is necessary other than to establish and enforce regulations to protect against over-use or excessive disturbance. This primarily involves the development and enforcement of harvest regulations. Hunting of ptarmigan is allowed for the sole purpose of providing recreational opportunity; it serves no function as a management tool for controlling ptarmigan populations. The alpine will not be over-populated with ptarmigan in the absence of hunting. To the contrary, hunting can suppress easily accessible ptarmigan populations that occur near major metropolitan areas. Because hunting is not a necessary management tool, it should be carefully regulated and monitored. Seasons must be established based on sound biological information that protects populations from over-harvest.

There have been numerous specific recommendations for the management of white-tailed ptarmigan populations and their habitats. The following recommendations are provided as a guide for resource managers and decision makers to consider when formulating management strategies to address the primary threats identified in this assessment.

Education and research

- ❖ Enhance the public's knowledge of alpine ecology and gain their support in dealing with the threats that human activities pose to the alpine ecosystem and its associated wildlife through education programs.

- ❖ Educate those sectors of the public whose land use practices and activities directly threaten ptarmigan populations and their habitats, and involve them in the development of management strategies to address the threats.

- ❖ Seek logistical and financial support from conservation organizations, such as the North American Grouse Partnership, Audubon Society, National Wildlife Federation, and The Nature Conservancy, in developing and implementing educational programs and conservation measures to protect ptarmigan populations and their habitats.

- ❖ Recognize that implementation of management actions must transcend political and jurisdictional boundaries to be effective.

- ❖ Develop protocols and educate the public about ethical wildlife viewing practices.

- ❖ Acknowledge that sufficient evidence exists to warrant concern about the individual and combined effects of global climate change, depletion of the ozone layer, nitrogen deposition, and accumulation of toxic compounds on the health of alpine environments; consider and address these environmental threats when developing long-range management plans for ptarmigan and alpine habitats.

- ❖ Advocate, support, and encourage more environmental research and monitoring programs on climate change, ozone depletion, nitrogen deposition, and accumulation of toxic chemicals in the alpine zone.

- ❖ Incorporate information into environmental education programs about the causes and effects of climate change, ozone depletion, nitrogen deposition, and accumulation of toxic chemicals in alpine ecosystems.

- Develop and implement pre- and post-treatment designs with controls and replications to increase the understanding of cause and effect relationships between land uses and changes in ptarmigan habitats and populations.

- Recognize that ptarmigan populations are affected by multiple factors and that the cumulative effects of these factors must be considered in formulating any future management actions.

Grazing

- Exercise extreme caution in permitting grazing of alpine ecosystems until scientific evidence is gathered that demonstrates grazing improves, restores, maintains, or at the very least, does not harm alpine plant communities.

- Exercise extreme caution in permitting livestock grazing of alpine ecosystems until (1) better indicators are developed for determining range readiness, (2) forage utilization can be accurately measured, and (3) appropriate standards are developed for assessing range condition and trends.

- Exercise extreme caution in permitting livestock grazing of alpine ecosystems until range managers have a better understanding of the process of plant succession in the alpine and the physiological responses and competitive interactions of alpine plants to grazing.

- Consider incorporating the following conditions when developing grazing plans for alpine allotments:
    - no grazing prior to 15 July or after 1 September
    - no grazing during drought years
    - no grazing of naturally dry and naturally wet sites
    - no grazing on slopes over 40 percent
    - no grazing of willow patches
    - no grazing of slopes holding late-lying snowfields regardless of their steepness.

- Address provisions for resting the allotment, monitoring the range, and enforcing the agreement in the allotment plan.

- Consider carefully range management principles and practices developed in other ecosystems before applying them to alpine areas.

- Prohibit any projects designed to reduce willow abundance and/or to increase grass production for livestock.

Mining

- Monitor cadmium levels in willow-dominated areas downstream from abandoned mines located in subalpine and alpine zones, especially within known ptarmigan winter use areas.

- Clean up abandoned mine sites within the subalpine and alpine zones.

- Use only native plant species in the restoration of disturbed alpine sites.

- Encompass more than revegetation in restoration attempts; also include efforts to mimic the natural contours and conditions (i.e., rock cover) of the landscape prior to disturbance.

- Recognize that restoration of the more extreme sites at high elevations and on steep slopes is beyond the capabilities of current technology, except for superficial kinds of cosmetic treatments.

- Recognize that restoration efforts will not fully restore ecosystem structure and function even on the most productive sites with well-developed topsoils.

Recreation and roads

- Identify and map areas of high recreational use in the alpine and work with recreational groups to develop mutually acceptable guidelines and regulations to minimize disturbance of ptarmigan and damage to ptarmigan habitats.

- Exclude winter recreational activities, such as snowmobiling and skiing, in willow-dominated sites above treeline and along stream courses immediately below treeline.

- Evaluate the status and condition of all roads in the alpine; carefully assess whether existing roads are necessary and reduce road densities whenever possible; consider other management options, such as seasonal closures, if complete closure is not possible.

- Close roads that are causing significant resource damage or have the potential to cause excessive damage because of their location (e.g., roads that traverse highly erosive slopes or wet areas); close any unplanned, unauthorized, or poorly designed roads.

- Prohibit the use of all four-wheel drive roads in ptarmigan use areas from 1 November to 1 July.

Habitat modification

- Discourage attempts to modify the distribution and amount of snow through the use of snow fences, cloud seeding, or other artificial means.

- Concentrate power lines along existing corridors rather than creating new corridors; remove any unused power lines; modify power lines that traverse critical ptarmigan habitats to minimize collisions and discourage use by raptors.

- Remove abandoned man-made structures at or above treeline that may serve as denning, nesting, or perching sites for predators.

- Evaluate carefully the location of any man-made features, such as power lines, roads, ski areas, reservoirs, and mine sites, in relation to ptarmigan habitat requirements and known ptarmigan use areas.

- Identify and protect corridors to maintain population connectivity.

- Identify and protect winter use areas.

- Allow no net loss of willow.

Population surveys and inventory

- Develop and implement a statewide system for monitoring ptarmigan populations; consider stratifying the areas surveyed by features such as hunting intensity (no hunting, lightly hunted, and heavily hunted), location (within and outside the ore belt), and use (grazed or ungrazed).

- Conduct surveys in southeastern (Snowy Range) and northwestern (Absaroka Mountains) Wyoming using tape-recorded calls to ascertain the presence or absence of breeding ptarmigan in these areas.

Hunting regulations and harvest surveys

- Close hunting seasons, where necessary, in easily accessible areas near human population centers.

- Close hunting seasons, where necessary, before mid-October when birds start arriving on wintering areas.

- Do not open hunting seasons before mid-September to insure juvenile grouse are old enough to survive independent of the brood hen.

- Explore new ways to increase the precision of harvest surveys, especially the ability to identify the sampling universe.

- Sample 100 percent of the hunters registering with the Hunter Information Program (Colorado) who say that they are likely to hunt ptarmigan.

Information Needs

Studies in Region 2 have provided essential information about the status, distribution, biology, life history, and ecology of white-tailed ptarmigan, but additional studies are needed to compliment this information. The primary information needed for effective conservation of white-tailed ptarmigan in Region 2 is a clearer understanding of how the species responds to alterations in habitat and changes in environmental conditions. A prerequisite for this understanding is the need for additional information on the micro-scale habitat selection patterns of ptarmigan, especially during the breeding and brood-rearing periods. In addition, aspects of the seasonal movement and dispersal patterns of ptarmigan need further investigation. This information is vital to understanding the spatial scale at which population exchange might occur. Large samples of radio-marked birds will be necessary to obtain this information. Given problems of locating birds that move the farthest, the search area cannot be restricted, and every effort must be made to locate and account for all radio-marked birds. Other aspects of movements also need further understanding. For example, it is suspected that ptarmigan may move between two or more wintering areas within the same winter and that some ptarmigan may not migrate during mild winters, but such movements are poorly documented.

Uncertainty remains about the precise distribution of ptarmigan in Region 2. No valid records exist to substantiate reports of ptarmigan in northwestern Wyoming. Surveys have failed to locate ptarmigan or evidence of their presence in this region of the state (Pattie and Verbeek 1966, Braun 1988, McEneaney 1995). Yet, several published distribution maps show that ptarmigan are present in northwestern Wyoming (Aldrich 1963, Johnsgard 1973, Braun et al. 1993). Despite the lack of evidence, at least one prominent grouse biologist believes ptarmigan may occur in low densities in the Absaroka Mountains (C.E. Braun personal communication, 2006). An effort needs to be made to confirm or refute the presence of ptarmigan in northwestern Wyoming using the play-back of tape-recorded calls during the spring breeding period.

An accurate range-wide assessment of the distribution and abundance of white-tailed ptarmigan and their habitats is critical for development, implementation, and evaluation of management or conservation plans. Towards this end, a standardized, statistically valid technique is needed to estimate white-tailed ptarmigan densities over broad geographic areas. The health of the population cannot be reliably ascertained based on surveys of small areas. Surveys must be designed to sample populations and habitats over large areas. This information is especially needed from states other than Colorado. For example, basically nothing is known about the status of the ptarmigan population inhabiting the Snowy Range in southeastern Wyoming. Some believe ptarmigan no longer occur there. Critical breeding, brood-rearing, and wintering habitats in southeastern Wyoming have yet to be delineated. It is uncertain whether in the past this population was self-sustaining or maintained by immigration of birds from Colorado. If immigration does occur, from where are the birds coming and by what route (i.e., travel corridor) are they getting there? What factors (i.e., habitat quality, patch size, grazing) are limiting this population? Is intervention (i.e., population augmentation, reintroduction) a viable management option?

In this assessment, an attempt was made to gather grazing information for all allotments within the alpine zone of Region 2. The information provided was incomplete and often difficult to decipher. Each individual Forest keeps its own grazing records, but there is no centralized database from which to assess the grazing status of all alpine areas within the Region. The grazing status of all alpine areas, including public and private lands, within the occupied range of white-tailed ptarmigan needs to be documented. Areas need to be classified as currently grazed, currently ungrazed but open to grazing, or permanently closed to grazing. Where possible, the grazing history of alpine allotments needs to be recorded. For example, how many years out of the past 50 has the area been subject to grazing and by how many and what type of livestock? If an allotment is currently ungrazed but open to grazing, when was the last time it was grazed?

Cadmium poisoning has been identified as a threat to ptarmigan populations in portions of Colorado (Larison et al. 2000, Larison 2001). Additional research and monitoring is required to verify the extent and magnitude of this problem. The ingestion of cadmium is occurring during the winter in willow-dominated habitats primarily used by females (Larison et al. 2000). Therefore, an effort needs to be made to locate and sample as many of these wintering areas as possible. High resolution satellite imagery and aerial photographs taken of alpine and subalpine areas during the winter (January, February, or March) are needed to aid in locating possible wintering areas for white-tailed ptarmigan. Likewise, imagery and photographs from early to mid-May would be beneficial in mapping breeding habitat for white-tailed ptarmigan.

The metapopulation model appears applicable to white-tailed ptarmigan (Martin et al. 2000). Thus, metapopulation dynamics of white-tailed ptarmigan in relation to the cadmium problem should be examined in further detail. Evidence suggests the only reason populations are maintained in cadmium-contaminated environments is through high rates of recruitment from less contaminated populations (Larison 2001). Further studies are necessary to ascertain if cadmium produces a mix of habitats, some healthy and some not, between which birds must actively recruit to maintain population viability.

Hunting as a possible factor contributing to the decline of local ptarmigan populations will likely become a contentious issue in the future. The merits of hunting are being increasingly challenged. The extent to which hunting is additive or compensatory remains debatable. Definitive experiments are needed to resolve this debate. Accordingly, there must be an ongoing effort to increase the precision of harvest estimates. Better information is needed on the distribution of the harvest so potential problem areas can be identified and regulations enacted to protect against over-harvest.

Food habit studies have focused on the adult segment of the population. Additional knowledge is required on the food habits of ptarmigan from the time of hatch until 5 weeks of age when they start eating the same foods as adults. Additional knowledge also is required about the influence of nutrient levels and secondary compounds on winter food selection. Ptarmigan in Region 2 depend on willow for food in winter, but it is highly unlikely that all willow plants are equally valuable as food. An understanding of the physical and chemical attributes of willow that ptarmigan select as food is critical to protecting and managing winter habitats. It also is important to know if the same factors that drive selection in winter also influence selection for willow during other seasons. Can a willow plant be poor or marginal food in one season and good food in another season? Are older plants preferred to younger plants? Within plants, are buds on new growth preferred to buds on older stems? Do ptarmigan select among different species of willow, and if so, which species are most preferred at different times of the year? Do winter food preferences differ between males and females?

Additional research is needed to develop restoration techniques for alpine areas that are better able to mimic pre-disturbance conditions. Full restoration has not been achieved even on small areas. Part of the problem is the lack of knowledge about the establishment ecology and competitive interactions of alpine plants, particularly for low-nutrient adapted forbs (Chambers 1997, Macyk 2000). In addition, data are lacking on the long-term effects of different restoration approaches, including choice of species used in the restoration and application of soil amendments. Most importantly, no studies have been conducted to monitor the response of wildlife to restoration efforts in the alpine.

New studies on ptarmigan should focus on applied research and move away from descriptive, correlative, short-term work on small geographic areas, to large-scale, long-term experiments that include treatments, controls, and replications. Data derived from such studies are critically lacking for ptarmigan. Well-designed experimental studies are essential for understanding the effects of grazing, recreation, mining, and global warming on ptarmigan populations and habitats. Ideally, these studies should be conducted in collaboration with scientists from other disciplines (e.g., plant ecology, climatology, hydrology, restoration ecology, toxicology). The recommendations resulting from these studies must in turn be tested through well-designed experiments to evaluate their effectiveness in achieving the desired outcome (adaptive management). It is only under this scenario that concrete recommendations can be developed for managing ptarmigan populations and their habitats. Recommendations developed under this scenario will have greater credibility and support among decision makers, and most importantly, a higher likelihood of being implemented than recommendations based only on descriptive studies.

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