CHARACTERISTICS OF A WINTERING POPULATION OF WHITE-TAILED PTARMIGAN IN COLORADO

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Information concerning White-tailed Ptarmigan (*Lagopus leucurus*) in winter is lacking primarily because of poor access, harsh environmental conditions, and insufficient effort by investigators to study them during this season. Some data on wintering populations of this species have been published (Braun and Schmidt 1971, May and Braun 1972, Moss 1973, 1974, May 1975), but most studies have pertained to behavior (Choate 1960, Schmidt 1969) and general population biology (Weeden 1959, Choate 1963, Braun 1969, Haskins 1969). In order to further understand the biology of this alpine grouse, we collected data opportunistically from 1966 through 1971 and intensively from 1972 through 1974. Objectives were to: (1) document departure and arrival from and to wintering areas, (2) describe sex and age composition of flocks, (3) examine flocking behavior and flock size, and (4) ascertain the affinity of marked birds for individual wintering sites.

STUDY AREA AND METHODS

Guanella Pass, situated in the Front Range of the Rocky Mountains in north central Colorado, was selected as the primary winter study area principally due to the abundance of wintering ptarmigan, accessibility, and availability of information on this area from prior studies (Schmidt 1969, Braun and Schmidt 1971, May and Braun 1972). The area studied encompasses approximately 9 km^2, an unusually large area compared to most known wintering grounds. In addition to studies at Guanella Pass, limited winter investigations were conducted near Waldorf, Naylor Lake, Steven's Gulch, and Horseshoe Basin where small numbers of ptarmigan winter. These sites are located within 3 to 13 km of Guanella Pass and vary in size from 2 to 4 km^2.

Winter use sites can be categorized as: (1) those at or above treeline generally at the head of a drainage, and (2) those below treeline along stream courses. Guanella Pass is an example of the former type of winter use site. Topography of this area is rolling with slopes ranging from 5 to 30% and elevations from 3475 to 3655 m above sea level. The vegetation is complex and may best be described as a mosaic of several communities, mostly dominated by willow (*Salix* spp.), which subtly intergrade with each other. Dominant communities are *Salix-Carex* wet meadows, *Salix* marshes, *Salix-Picea* Krummholz, and *Carex-Trifolium* meadows. Most of the area is snow covered during winter, with snow depths varying considerably. While snow cover is normally in excess of 95%, portions of the area are exposed to prevailing westerly winds. Consequently, bushes of willow are rarely completely snow covered.

Winter groups of ptarmigan were located by concentrated searching on foot with periodic stops to scan surrounding areas for tracks, snow roosts, and/or birds. Upon locating a flock, we tried to count all birds present. Some bias resulted when all birds present could not be counted. This bias was most serious (1) when 30 or more birds

were dispersed over a large area such that all individuals could not be seen, (2) when the birds were in snow roosts, and (3) when the flock flushed before all members could be counted. In such instances, only minimum estimates of flock size were obtained. Following Koskimies (1957), 2 or more grouse constituted a flock.

After obtaining counts of flock size, birds were observed through 7×50 binoculars in order to ascertain banded to unbanded ratio and to identify marked individuals. Some unbanded ptarmigan and all birds with unreadable bands were pursued until caught or flushed and not relocated. Observations were recorded at the time on standardized cards and locations were subsequently plotted on 7.5 minute U.S. Geological Survey topographic maps.

Ptarmigan were captured with a 5 or 7 m telescoping noose pole as described by Zwickel and Bendell (1967) for Blue Grouse (*Dendragapus obscurus*) and modified by Braun and Rogers (1971) for White-tailed Ptarmigan. Captured birds were banded and classified to age and sex following methods presented by Braun and Rogers (1971). Age categories used were adult (including subadults [1+]), and juvenile (less than 1 yr old).

RESULTS AND DISCUSSION

Arrival and departure.—Winter on the alpine was arbitrarily designated as the period beginning in late October when ptarmigan became entirely white through mid- to late April when the prenuptial molt of males was initiated. In 1971–72 and 1973–74, most birds started arriving on the wintering area by 20 to 26 October and remained until 19 to 30 April when they departed for breeding areas. Birds did not arrive or depart simultaneously; movements to and from winter use sites were gradual extending over a 2-week period. However, climatic conditions had a pronounced influence upon arrival and departure. Prolonged mild weather during the fall of 1972 delayed arrival until 3 to 5 November while extended winter conditions the following spring (1973) delayed departure until 3 to 10 May.

Sex and age composition.—We identified 799 ptarmigan at Guanella Pass from from 1966 through 1974. There were significantly more ($P < 0.005$) adults than juveniles identified, but the proportion of the total birds handled in each age class was not consistent among winters (Table 1). This variation was attributed to differences in nesting success among years. During the summer of 1972, 37 (82.2%) of 45 females encountered on breeding areas surrounding Guanella Pass were accompanied by chicks, whereas in 1973 only 19 (54.2%) of 35 hens located were with broods (Hoffman 1974). Juveniles comprised 42.3 and 27.2% of the birds identified at Guanella Pass during the 1972–73 and 1973–74 winters, respectively, supporting the hypothesis that more juveniles (percent of total identified) occur on the wintering area following summers of good production than after summers of poor production.

Partial segregation of sexes has been documented at Guanella Pass (Braun and Schmidt 1971); however, both sexes are not equally represented on the wintering area. Significantly more ($P < 0.001$) females than males were identified each winter (Table 1), but the proportion of males and females

TABLE 1

SEX AND AGE COMPOSITION OF WHITE-TAILED PTARMIGAN WINTERING AT GUANELLA PASS

Winter[1]	N[2]	% Adults	% Juveniles	% Females	% Males
1967–68	66	54.5	45.5	72.7	27.3
1968–69	43	70.0	30.2	81.4	18.6
1969–70	111	78.4	21.6	78.4	21.6
1970–71	125	61.6	38.4	80.8	19.2
1971–72	142	56.3	43.7	78.9	21.1
1972–73	153	57.7	42.3	77.4	22.6
1973–74	125	72.8	27.2	84.0	16.0
Total	765				
Mean		64.5	35.5	79.0	21.0

[1] The winter of 1966–67 was excluded due to small sample size (34 birds identified).
[2] Total number of birds identified.

occupying the area between winters was not significantly different ($P > 0.50$). Nearly 80% of the estimated 200 to 300 grouse annually wintering at Guanella Pass were females.

Suitable wintering areas for female ptarmigan, such as Guanella Pass, appear to be limited in number; consequently, females from considerable distances are attracted to the few suitable sites (Hoffman and Braun 1975). Areas used by males during winter are scattered throughout the alpine region and each area need only support a small number of males breeding in the immediate vicinity. Winter studies in Colorado indicate that partial segregation of sexes is not unique to the Guanella Pass area. This phenomenon is not only characteristic of White-tailed Ptarmigan as Weeden (1964) reported evidence of sexual segregation in both Rock (*L. mutus*) and Willow ptarmigan (*L. lagopus*). Additional evidence of sexual segregation in Willow Ptarmigan was reported by Irving et al. (1967).

Segregation of sexes of White-tailed Ptarmigan may only be spatial, but generally a difference in habitat preference occurs. Extensive stands of willow do not grow in some locations while in others, the willow may be completely snow covered in winter. Frequently this situation and/or poor snow conditions (lack of available roosting sites) forces both sexes to move below treeline along stream courses. Under these circumstances females were found to winter farther down the same drainage than males; a purely spatial separation. In segregation by habitat, males winter in Krummholz areas alternately dominated by clumps of willow and Engelmann spruce (*Picea engelmannii*). Food availability in these sites is largely dependent upon wind action. Females winter at lower elevations near or at treeline where dense,

tall stands of willow grow. Regardless of whether the separation was spatial or an actual difference in habitat preference, males showed a strong tendency to winter closer to breeding areas than females.

Available information concerning segregation of sexes is primarily oriented towards the descriptive aspects of this behavior pattern with no explanation for its occurrence. Obviously there must be an adaptive advantage for sexes to live separately during the winter. Weeden (1964) suggested that another process, migration, must be investigated in detail before segregation of sexes in Rock and Willow ptarmigan could be understood. He also suggested that due to the more sedentary nature and apparently non-migratory behavior of White-tailed Ptarmigan, possibly the 2 processes could be studied independently of each other with this species. However, studies of White-tailed Ptarmigan in Colorado reveal they are migratory and that the processes are very closely related (Hoffman and Braun 1975). The fact that most females traverse long distances to seek out suitable winter habitat and return to the same area year after year is a strong manifestation of migration and that conditions are better for winter survival in these limited areas to offset increased mortality during migration. Principal advantages of wintering in these limited sites appear to be the presence, abundance, and availability of willow which comprises about 89% of the winter diet (May and Braun 1972) and secondarily proper snow conditions for roosting.

It is unclear what advantages are gained by males wintering in exposed sites adjacent to breeding areas and not undergoing long migrations typical of females. No marked differences occur in winter diets of the sexes to necessitate separation (May and Braun 1972). However, food resources are not sufficient at high elevations to support large numbers of wintering birds. Thus it would appear advantageous for survival that a segment of the population migrate to areas where food is abundant. Under Colorado conditions, ptarmigan not only gained weight throughout the winter, indicating no food shortage (Braun and Schmidt 1971, May 1975), but also more efficiently used the winter resources that were available. Possibly it is advantageous for male ptarmigan to winter adjacent to areas where they breed in order to successfully compete for territories the following spring.

Flocking behavior.—Like most grouse, ptarmigan are gregarious, associating in flocks most of the year. Flocks are temporarily fragmented from late April until mid-July due to breeding activities. Flocking tendencies are most evident from late October to late April when ptarmigan are concentrated on winter use sites. From 1966 through 1974, 172 winter flocks and 13 lone ptarmigan totaling over 3178 birds were observed on the Guanella Pass wintering area.

Winter flock size varied from fewer than 5 to over 80 birds. Number and

TABLE 2

YEARLY TRENDS IN FLOCK SIZE OF WHITE-TAILED PTARMIGAN AT GUANELLA PASS

Year[1]	No. flocks observed	No. birds involved	Mean yearly flock size	Yearly range in flock size
1969–70	29	342	11.8	2–50
1970–71	23	340	14.9	3–42
1971–72	29	432	14.9	2–40
1972–73	33	689	20.9	2–75
1973–74	21	316	15.0	2–80

[1] Data from winters of 1966–67, 1967–68, and 1968–69 were excluded due to small sample sizes (< 15 flocks observed per winter).

frequency of encounters of 172 winter flocks and 13 lone birds were as follows: (1) 13 (7.0%) lone birds, (2) 127 (68.7%) flocks with 2 to 25 individuals, (3) 35 (18.9%) flocks with 26 to 50 individuals, and (4) 10 (5.4%) flocks with more than 50 individuals. Flocks of males were small (< 15 birds) while females typically congregated in flocks of larger size (20 to 30 birds). Only infrequently were ptarmigan observed singly, indicating their highly social nature during the winter period.

Mean flock size was not significantly different ($P > 0.05$) among winters for the 5 winters of 1969–74 (Table 2). The 135 flocks observed over the 5 winters averaged 15.5 birds. Similarly, mean flock size did not differ significantly ($P > 0.05$) among the 7 winter months, as average flock size varied from 16.0 to 23.8 birds (Table 3). Flocks tended to be smaller in October and April being 16.0 and 16.2 birds per flock, respectively. Both months represent transition periods when birds are either arriving on (October) or departing from (April) winter use sites. Since birds do not

TABLE 3

MONTHLY TRENDS IN FLOCK SIZE OF WHITE-TAILED PTARMIGAN AT GUANELLA PASS

Months[1]	No. flocks observed	No. birds involved	Mean monthly flock size	Monthly range in flock size
Oct.	8	128	16.0	12–30
Nov.	27	644	23.8	3–60
Dec.	30	664	22.1	2–80
Jan.	30	510	17.0	2–70
Feb.	18	316	17.6	4–75
Mar.	28	491	17.5	2–75
Apr.	31	501	16.2	2–60

[1] Pooled data for winters of 1966–67 through 1973–74.

arrive or depart simultaneously, fewer birds were present at these times to form flocks.

Koskimies (1957) suggested increased population numbers of Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*) and good nesting success led to larger flocks, and to a lesser degree, more flocks. Considering the failure to detect a significant difference in mean flock size among years, even though nesting success varied from year to year, there was no indication that nesting success influenced winter flock size of White-tailed Ptarmigan. However, 2.37 flocks were observed per day on the wintering area following the good production in 1972, while only 1.29 flocks were located per day following the poor production in 1973. Assuming more birds are present on a wintering area after a summer of good production, they apparently form more flocks instead of gathering into larger flocks.

Winter flocks were not composed of family units nor did the same individuals associate together throughout the winter. Ptarmigan broods disperse in late September or early October (Braun 1969) prior to their arrival on wintering areas. No females nor any of their chicks banded together during the summer were relocated in the same winter flock. Considerable interchange of birds occurred between flocks with no noticeable aggressive behavior exhibited towards new flock members. Although exact numbers cannot be cited, many individual birds banded at Guanella Pass were relocated several times throughout the winter associating with flocks of various sizes comprised of different individuals at different locations.

Affinity for wintering areas.—Data obtained from 90 birds initially banded at Guanella Pass and subsequently relocated on breeding or summering sites were used to ascertain the affinity of individual birds for the wintering area. The sample included 62 females and 28 males of which 45 (50.0%) returned in succeeding winters. A bird needed only to return once to be included in the sample, but some individuals returned up to 4 consecutive winters. Occasionally there was an intervening winter when a marked bird was not observed. Birds in this category were probably present on the wintering area but not located.

Fifteen of the 45 birds failing to return were known to be lost from the population (12 hunting mortalities, 2 collections, and 1 trapping mortality) before having a chance to return. To obtain a more accurate estimate of the percentage of birds returning that were available, the 15 birds having no opportunity to return were excluded. Consequently, the sample consisted of 75 birds (22 adult females, 32 juvenile females, 8 adult males, and 13 juvenile males) with at least 45 (60.0%) returning. This estimate must be considered conservative since it was assumed that all birds not returning were either dead or wintering elsewhere; whereas, possibly some birds returned that were

not located. Thus, ptarmigan demonstrate a high fidelity to wintering areas similar to their attachment to breeding sites (Schmidt 1969).

Using a 2×2 contingency table, differences between the number of birds returning were tested for adults vs juveniles, males vs females, juvenile females vs adult females, and juvenile males vs juvenile females. Comparisons involving adult males were not possible because of small sample size (expected frequencies less than 5; Simpson et al. 1960). Number and frequency of each age and sex class returning were as follows: 16 (72.7%) adult females, 17 (53.1%) juvenile females, 6 (75.0%) adult males, and 7 (46.2%) juvenile males. No comparisons were statistically significant ($P > 0.05$); however, for the pooled sample of both sexes the comparison between adults vs juveniles closely approached significance (< 0.055). In all cases, proportionally more adults (73.3%) than juveniles (51.1%) returned. Juveniles suffer higher mortality than adults (Braun 1969); consequently, fewer are available to return. In addition, juveniles have no prior attachment to breeding sites and upon leaving the wintering area in spring they frequently travel long distances in search of vacant territories where they can become established as breeding birds (Hoffman 1974). Some of these birds probably winter closer to their territories and do not return. Of 40 birds identified on other nearby winter use sites, 4 (10%) were originally banded at Guanella Pass. All were banded as juveniles. Although the sample is small, it does indicate that ptarmigan banded as juveniles are more likely to disperse from wintering areas where they were initially banded and subsequently winter elsewhere.

No differences were apparent in the proportion of adult males (75.0%) and females (72.7%) returning to Guanella Pass. Based on the return of marked birds to breeding territories, Braun (1969) reported a 25 and 30% annual turnover of adult males and females, respectively. Annual turnover of adult males and females estimated by Braun (1969) is similar to the mortality rates for birds wintering at Guanella Pass indicated by data collected in this study. Since adults show a high fidelity to wintering sites, it can be reasonably assumed that most not returning are dead; consequently, percentage of non-returning adults approximates annual turnover rates. A similar assumption cannot be made for juveniles because non-returning juveniles are not necessarily lost from the population. Also, percent of birds not returning cannot be considered an approximation of annual turnover for the entire population as loss of chicks prior to their arrival on the wintering area is not included.

SUMMARY

Studies of the characteristics of a wintering population of White-tailed Ptarmigan were conducted in alpine areas in north central Colorado, primarily at Guanella Pass. Of 799 Ptarmigan identified on the wintering area, 80% were females and 65% were adults. Numbers of juveniles identified varied with year depending upon production success.

Climatic conditions had a pronounced influence upon the timing of arrival and departure to and from winter use sites. Partial segregation of sexes coincided with the arrival of birds on wintering areas with males usually remaining closer to breeding areas. Large concentrations of females wintered in areas at lower elevations near treeline where dense, tall stands of willow occurred. At times sex separation was only spatial, but usually habitat separation occurred.

Winter flocks ranged in size from 2 to over 80 birds with about 69% of all flocks (172) encountered consisting of 2 to 25 members. Flock sizes did not change significantly among years or months. Following a summer of good production, ptarmigan formed more flocks instead of gathering into larger groups. Due to greater mobility and higher mortality, fewer juveniles than adults returned in subsequent winters, but all age and sex classes exhibited a high fidelity (60% return) to the wintering area.

ACKNOWLEDGMENTS

We acknowledge the support and direction given this study by R. A. Ryder, Department of Fishery and Wildlife Biology, Colorado State University, and H. D. Funk of the Colorado Division of Wildlife. T. A. May, Institute of Arctic and Alpine Research, University of Colorado, and A. E. Anderson, Colorado Division of Wildlife, accompanied us and helped gather data during several field periods. The National Science Foundation supported this study in part from 1966 through 1969 through a traineeship to the junior author while the Colorado Division of Wildlife supported it throughout its duration. This is a contribution from Colorado Federal Aid in Wildlife Restoration Project W-37-R.

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WILDLIFE RESEARCH CENTER, P.O. BOX 2287, FORT COLLINS, CO 80522. ACCEPTED 17 FEB. 1976.