Wilson Bull., 104(2), 1992, pp. 263–272

WINTER HOME RANGE AND HABITAT CHARACTERISTICS OF WHITE-TAILED PTARMIGAN IN COLORADO

KENNETH M. GIESEN AND CLAIT E. BRAUN[1]

ABSTRACT.—Home ranges, habitat characteristics, and fidelity of White-tailed Ptarmigan (*Lagopus leucurus*) to wintering sites were studied in north-central Colorado. Winter home ranges of 17 hens averaged 1.62 ± 0.72 km^2 and were larger than those of two males (0.44 ± 0.20 km^2). Home ranges of four radio-marked hens averaged 2.44 km^2. Percent canopy cover of willow (*Salix* spp.) was higher at ptarmigan feeding sites than at random sites when combining samples for the entire winter, but did not differ during March and April when snow depth was greatest. Crude protein of willow buds, the primary winter food, averaged 10.28% and did not differ between random and feeding sites or between fed-upon and non-used willow within a feeding site. Ptarmigan hens showed high fidelity to home ranges used in previous winters. *Received 12 April 1991, accepted 23 Oct. 1991.*

White-tailed Ptarmigan (*Lagopus leucurus*) are an important component of alpine avifaunal communities in the central and northern Rocky Mountains of North America and are one of the few resident species (Braun 1980). Previous studies of White-tailed Ptarmigan have provided information on breeding behavior and biology, population dynamics, and summer habitat characteristics (Choate 1963; Braun and Rogers 1971; May and Braun 1972; Herzog 1977; Giesen and Braun 1979a, b; Giesen et al. 1980; Hoffman and Giesen 1983; Schmidt 1988). Studies of wintering White-tailed Ptarmigan have described their habitats, migration, and flock characteristics (Braun and Schmidt 1971; Braun et al. 1976; Hoffman and Braun 1975, 1977; Herzog 1980).

We quantified home range size and documented patterns of habitat use in relation to food resources by a wintering population of White-tailed Ptarmigan in Colorado. Home range is a measure of the area used by an animal for its normal activities (Burt 1943) but may also be an index to energetic costs or habitat quality. Home range size also has implications for understanding minimum habitat patch size to sustain an individual or population.

STUDY AREA AND METHODS

We studied ptarmigan at Guanella Pass (39°35'N, 105°42'W), along the Front Range of the Rocky Mountains in north-central Colorado, during winter 1982–1983. Guanella Pass has been the site of several previous studies of White-tailed Ptarmigan (Schmidt 1969; Braun and Schmidt 1971; May and Braun 1972; Hoffman and Braun 1975, 1977) and is a willow

[1] Colorado Div. of Wildlife, 317 W. Prospect Rd., Fort Collins, Colorado 80526.

(*Salix* spp.)-dominated drainage at treeline (elevation 3475–3655 m). Approximately 10 km^2 of wintering habitat comprised the study area. This site is used each winter by 100–200 ptarmigan, primarily females (Hoffman and Braun 1977).

Climatic conditions of the Colorado Front Range have been described by Marr (1961), Judson (1965), and Marr et al. (1968) and are best characterized as continental, with wind speeds and snow depths increasing from October through late March–early April. Temperature and snowfall data were obtained from a National Oceanic and Atmospheric Administration weather station at Berthoud Pass (elevation 3448 m), approximately 23 km north. Snowfall was recorded on 139 of 211 days (65.9%) between 1 October 1982 and 30 April 1983; total snowfall for winter 1982–1983 (1233 cm) was 125% of the 15-year average. This was primarily the result of high snowfall from March to May and was not believed to have affected ptarmigan behavior or movements except for possibly delaying their departure from the wintering area. Recorded temperatures varied little from the long-term average.

We looked for ptarmigan on foot and used binoculars to scan for birds, tracks, roosts, and fecal droppings. Radio-telemetry equipment was used to locate specific birds (N = 6) and associated flocks throughout the winter. Flock size was recorded and previously captured birds were identified from their unique combinations of colored bands. Ptarmigan were classified as to age and sex following Braun and Rogers (1971); ages of birds >two years old were based on initial date of capture. Efforts were made to capture unbanded birds using wire snares on telescoping fiberglass poles (Zwickel and Bendell 1967, Braun and Rogers 1971). Locations of ptarmigan were recorded on a standardized form and later plotted on a topographic map (scale 1:24,000) to obtain Universal Transverse Mercator (UTM) coordinates to the nearest 50 m.

Three home range estimators were computed using the McPAAL software package (M. Stuwe and C. E. Blohowiak, Conserv. Res. Cent., Natl. Zool. Park, Smithsonian Inst., Front Royal, Virginia, 1985): the convex polygon method (Mohr 1947), Koeppl et al.'s (1975) 95% ellipse, and Dixon and Chapman's (1980) harmonic mean. With the harmonic mean, a 10 × 10 grid was used with a 95% estimator. Home ranges were calculated only for birds observed ≥10 times (one per day, maximum) and for those individuals initially observed prior to 25 November 1982 and with a last observation after 30 March 1983. Hoffman and Braun (1977) reported that ptarmigan began arriving on this wintering area in late October and remained until mid-April, thus most birds studied had likely spent the entire winter at Guanella Pass.

The minimum convex polygon home range estimate was used because it included all observations of birds and wasn't biased by assumptions about random movement (independent observations) of birds within their home ranges. Because it is dependent upon sample size (Jennrich and Turner 1969), it provided a conservative estimate of area used by ptarmigan in our study. The 95% ellipse assumes the most probable location of an individual is at the center of the ellipse, and the probability of observing it decreases as the ellipse increases. This method is not sensitive to sample size and assumes the animal moves randomly about its home range. The harmonic mean has been shown to be less biased (Boulanger and White 1990) but also was among the least precise. These latter two methods are based on 95% probabilities, require assumptions about home range shape, and may eliminate some locations which may be important in understanding home range or habitat use.

Willow height, height above snow, canopy cover (Canfield 1941), and snow depth were recorded at ptarmigan use and randomly selected sites within the study area. Random sites were chosen using a table of random numbers to select UTM coordinates within the wintering area. Canopy cover was measured at snowline instead of at ground level, thus canopy cover at some sites varied with snow depth. At ptarmigan use sites, plots were centered at the greatest concentration of birds or tracks and 5-m transects were established in each of the cardinal compass directions. A 3-g sample of willow buds was collected from plants that had been fed upon and from plants not fed upon by ptarmigan at feeding sites and from willow plants at randomly selected sites. Nitrogen content of willow buds was ascertained using micro-Kjeldahl analysis (Horwitz 1980).

Mann-Whitney *U*-tests (Daniel 1978) were used to compare differences in home range sizes among classes of birds, to test for habitat differences between feeding and random sites, and to test for habitat differences among months. Differences in crude protein between fed-upon and non-fed-upon plants within sites were compared using paired *t*-tests (PROC MEANS; SAS Inst., Inc. 1988) and between feeding and random sites using *t*-tests (PROC TTEST; SAS Inst., Inc. 1988).

RESULTS

Home range size.—Forty-six of 115 ptarmigan individually identified during winter 1982–1983 were located initially prior to 25 November. Although most (N = 40, 87.0%) were observed later that winter, only 17 hens and two males were seen ≥ 10 times and observed at least through 31 March, thus providing minimum estimates of winter home range. The minimum convex polygon provided the most conservative estimate (Table 1) and was used for analysis. Individual winter home ranges of 17 hens averaged 1.62 ± 0.72 km^2 (mean ± SD) and were larger ($P < 0.005$) than those of two males (0.44 ± 0.20 km^2). The combined home range for the 17 hens was 7.33 km^2, or about 73% of the available winter habitat at Guanella Pass. Since these 17 hens represented <15% of the wintering population and the minimum convex polygon is a minimum home range estimate, it appears likely that most of the area was used by ptarmigan sometime during winter.

The number of observations did not appear to affect our estimates of home range among these 17 hens ($r = 0.302$, $P = 0.238$). Most (13 of 17) were located at least monthly, but there was no difference in home range size between these hens and four that were not observed every month ($P > 0.10$). Four radio-marked hens were included in the sample; these had larger home ranges than the other hens (2.44 vs 1.37 km^2; $P < 0.025$), which likely resulted from our ability to locate them after they moved to locations we seldom searched. Home range size of hens was not related to their age ($r = 0.023$, $P = 0.934$).

The minimum convex polygon provided the smallest estimate of home range. The harmonic mean estimate of average home range size for 17 hens was 45% larger, and the 95% ellipse estimate was 160% larger than the minimum convex polygon. A similar pattern was observed when using home ranges from four radio-marked hens.

Sightings of 15 adult female ptarmigan for which we calculated winter home ranges were within their individual home ranges for 100 of 114

TABLE 1
WINTER HOME RANGE ESTIMATES FOR WHITE-TAILED PTARMIGAN AT GUANELLA PASS, COLORADO, 1982–1983

Band	Age (years)	Sex	Dates observed	N obs.	Home range size (km^2) MCP[a]	Harmonic mean	95% ellipse
1832	12	F	09 Nov–20 Apr	37	1.43	1.95	2.42
2947	6	F	04 Nov–20 Apr	15	0.76	1.02	2.60
3259	6	F	24 Nov–15 Apr	10	2.04	3.84	9.33
3520[b]	6	F	09 Nov–15 Apr	31	3.90	6.32	9.47
3544	5	F	09 Nov–18 Apr	17	1.10	1.46	3.24
3693	5	F	21 Oct–18 Apr	32	1.34	1.57	2.49
3782	3	F	10 Nov–20 Apr	15	0.81	0.87	2.51
3786	4	F	09 Nov–18 Apr	22	1.14	1.21	3.32
3927	4	F	21 Oct–07 Apr	15	1.12	2.39	3.25
3928[b]	3	F	22 Nov–15 Apr	54	1.87	1.94	3.24
3929[b]	3	F	04 Nov–18 Apr	56	1.95	2.14	3.46
3930[b]	3	M	04 Nov–22 Apr	11	0.64	1.04	2.87
3931	3	F	09 Nov–20 Apr	34	1.62	1.94	3.04
3997	2	F	11 Oct–19 Apr	22	1.56	1.69	3.69
3999[b]	2	F	04 Nov–21 Apr	23	2.05	2.81	6.49
4096	2	F	11 Oct–31 Mar	18	1.46	2.09	4.19
4150	1	F	04 Nov–11 Apr	16	2.03	3.43	4.61
4153	1	M	16 Nov–21 Apr	12	0.24	0.39	0.95
4155	1	F	24 Nov–15 Apr	13	1.38	3.20	4.35

[a] Minimum convex polygon (Mohr 1947).
[b] Radio-marked.

observations (87.7%) during previous winters. Furthermore, 11 of these hens were identified at the Guanella Pass wintering area each year since being banded, and four were missed in only one year. It is likely these four hens were present each year also but were missed, since we spent fewer days searching for ptarmigan at Guanella Pass prior to 1982–1983.

Habitat characteristics.—Habitat characteristics were measured at 26 ptarmigan feeding sites and 21 randomly selected sites (Table 2). Because feeding sites were measured throughout winter (2 Dec–20 Apr) and randomly selected sites were measured only in March and April, direct comparison of snow depth and height of willow above snow could not be made from December to February. When comparing use sites with randomly selected sites for March and April, snow depth and willow height above snow differed in March only (Table 2).

Willow canopy cover and height above snow at feeding sites typically differed among months (Table 2) and was higher ($P = 0.0029$) at ptarmigan feeding sites than at random sites when all samples were combined. Height

TABLE 2
CHARACTERISTICS OF WHITE-TAILED PTARMIGAN FEEDING AND RANDOM SITES, GUANELLA PASS, COLORADO, 1982–1983

	Snow depth (cm)			Willow height above snow (cm)			Willow canopy cover (%)		
Month	$\bar{x}$	SD	N	$\bar{x}$	SD	N	$\bar{x}$	SD	N
December									
Feeding site				13.3	5.8	3	15.8[a,b]	4.0	3
January									
Feeding site	34.1	11.3	3	27.7[a]	9.6	3	37.1[a,b,c]	11.1	3
February									
Feeding site	42.8	12.6	7	26.0[b]	8.3	7	25.6[e,f]	12.1	3
March									
Feeding site	39.6*	26.1	6	8.0*[a,b]	2.9	6	8.8[a,c,e]	3.3	6
Random site	85.0	13.4	7	16.3	9.7	7	8.6	6.4	7
April									
Feeding site	72.3	23.9	7	12.4[b]	3.0	7	8.2[b,d,f]	4.3	7
Random site	86.7	21.9	14	15.3	5.3	14	6.7	4.1	14

* Means between feeding and random sites differ, Mann-Whitney test, $P < 0.05$.
[a,b,c,d,e,f] Means within a column sharing a letter are different, Mann-Whitney test, $P < 0.05$.

above snow generally decreased from January to April, which reflected increasing snow depths. Similarly, canopy cover declined during the same period, a reflection of less exposed canopy cover as snow depth increased.

Crude protein did not differ between buds from willow shrubs fed upon by ptarmigan and those nearby which were not fed upon, or those from randomly selected sites (Table 3). The overall level of crude protein was 10.28%.

DISCUSSION

Although we did not detect a significant correlation between individual winter home range size and number of observations, our data were biased by non-random distribution of ptarmigan and search patterns. Access to Guanella Pass was fortuitously adjacent to areas preferred by ptarmigan early and late in winter, and this area was searched on most trips to the area. Thus, birds that used this area were seen more often than those which dispersed throughout the wintering site. We believe the larger home ranges of radio-marked birds represent the most accurate estimate of White-tailed Ptarmigan winter home range size.

The smaller winter home ranges of the two males reflected their pref-

TABLE 3
CRUDE PROTEIN LEVELS OF WILLOW BUDS AT GUANELLA PASS, COLORADO, 1982–1983

Site	Crude protein (%) Mean	SD	N
Feeding sites	10.39[a]	0.17	37
Fed-upon plants	10.46[b]	0.82	17
Non-fed-upon plants	10.35[b]	1.31	17
Random sites	10.14[a]	0.15	29

[a] Crude protein did not differ, $P = 0.2635$.
[b] Crude protein did not differ, $P = 0.7339$.

erence for different winter habitats (Hoffman and Braun 1977) and their tendency to remain in small flocks throughout winter (Braun and Schmidt 1971). This spatial and habitat segregation may reflect a strategy of males to winter adjacent to breeding territories, thus reducing competition for resources in winter habitats.

Winter home range sizes are not well documented for grouse. Reported winter home range sizes of Greater Prairie-Chickens (*Tympanuchus cupido*) range from 8.4 km^2 (Toepfer and Eng 1988) to <0.4 km^2 (Robel et al. 1970, Schroeder and Braun 1992). Winter home ranges of Blue Grouse (*Dendragapus obscurus*) were <0.2 km^2 (Cade 1985, Hines 1986) and those of Spruce Grouse (D. *canadensis*) <0.1 km^2 (Herzog and Boag 1978). If size of winter home range is related to flock size, then increased winter flock size and home range may be a consequence of open habitats and dispersed winter food resources that are spatially separate from secure roosting habitat.

Fidelity of White-tailed Ptarmigan to wintering areas has been reported previously (Braun et al. 1976, Hoffman and Braun 1977). Our data indicate White-tailed Ptarmigan also show fidelity to individual winter home ranges. The benefits of such fidelity may include knowledge of roosting and foraging sites or may confer competitive advantages through dominance when feeding.

Densities of White-tailed Ptarmigan at Guanella Pass in winter averaged 10–20 birds/km^2, which is twice their mean density on breeding ranges (Braun and Rogers 1971). However, breeding territories are defended by paired birds whereas ptarmigan in winter are typically associated with flocks of 12–21 birds (Braun et al. 1976). Flocking of grouse in winter may be advantageous for obtaining or sharing information on food distribution and may also serve as a tactic for predator detection, which may increase survival of flock members (Bergerud and Gratson 1988). Flock composition and membership constantly changed throughout the winter, thus individual ptarmigan had contact with a large proportion of the local wintering population. Large home-ranges shared with conspecifics may result in decreased costs of defending abundant and dispersed food resources and allow for use of suitable snow roosting sites, which change in response to snow and wind conditions.

Willow buds, the primary winter food of White-tailed Ptarmigan in Colorado (May and Braun 1972), were available throughout the winter at Guanella Pass. Previous studies also indicated that food quantity (gross energy) and nutrient availability were not limiting to ptarmigan on a willow diet in winter (May 1975). White-tailed Ptarmigan gain weight during the winter period (May 1975; C. E. Braun, unpubl. data), which also suggests that food is not limiting in areas they occupy.

Whether ptarmigan exercised any selection for winter food was not determined, but no selection based on crude protein was observed. Our measure of crude protein was similar to that reported previously for White-tailed Ptarmigan in winter (9.5%, May 1975) and within the range reported in the winter diets of other grouse (Hoffmann 1961, Ellison 1966, Korshgen 1966, Moss 1968, Huff 1970, Pendergast and Boag 1971, Gasaway 1976, Gurchinoff and Robinson 1972, Pulliainen 1978, Remington 1983). Andreev (1988) reported that 10% crude protein was optimal for winter diets of Palaearctic grouse.

Suitable winter habitats for White-tailed Ptarmigan appear limiting (Hoffman and Braun 1975, Braun et al. 1976, Herzog 1980), primarily because of extreme weather conditions in alpine environments and high snowfall which limits food resources. Ptarmigan have adapted to this environment by migrating to areas where food is abundant (Hoffman and Braun 1975), and adopting behaviors and seeking microenvironments to minimize energy expenditures (Braun and Schmidt 1971).

All suitable habitats at Guanella Pass appeared to be used by ptarmigan in winter; the specific areas used changed in response to snow accumulation which affected snow roosting sites and food availability and abundance (Braun and Schmidt 1971). Localized food depletion, competition with conspecifics, snowfall, and availability of suitable conditions for snow roosting may contribute to daily and monthly movements during winter.

ACKNOWLEDGMENTS

We appreciate the assistance of E. Ernst and K. Duncan with trapping, banding, and collecting movement and habitat data during difficult weather conditions. K. Duncan also assisted with mapping locations for home range estimation. T. Remington conducted chemical analysis of willow buds and contributed to our understanding of grouse nutrition and energetics. We also thank D. Reed, M. Schroeder, M. Scymczak, and F. Zwickel for critical review of this manuscript. Permission to establish a field camp in the Arapaho National Forest, which facilitated data collection, was granted by T. Portice, Clear Creek District, Arapaho and Roosevelt National forests. This is a contribution from Colorado Federal Aid in Wildlife Restoration Projects W-37-R and W-152-R.

LITERATURE CITED

ANDREEV, A. V. 1988. Ecological energetics of Palaearctic Tetraonidae in relation to chemical composition and digestibility of their winter diets. Can. J. Zool. 66:1382–1388.

BERGERUD, A. T. AND M. W. GRATSON. 1988. Survival and breeding strategies of grouse. Pp. 473–577 *in* Adaptive strategies and population ecology of northern grouse (A. T. Bergerud and M. W. Gratson, eds.). Univ. Minnesota Press, Minneapolis, Minnesota.

BOULANGER, J. C. AND G. C. WHITE. 1990. A comparison of home range estimators using Monte Carlo simulation. J. Wildl. Manage. 54:310–315.

BRAUN, C. E. 1980. Alpine bird communities of western North America: implications for management and research. Pp. 280–291 *in* Workshop proc. management of western forests and grasslands for nongame birds (R. M. Degraff and N. G. Tilghman, compilers). U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. INT-86.

——— AND G. E. ROGERS. 1971. The White-tailed Ptarmigan in Colorado. Colorado Div. Game, Fish and Parks. Tech. Publ. No. 27.

——— AND R. K. SCHMIDT, JR. 1971. Effects of snow and wind on wintering populations of White-tailed Ptarmigan in Colorado. Pp. 238–250 *in* Proc. snow and ice symp. (A. O. Haugen, ed.). Iowa State Univ., Ames, Iowa.

———, R. W. HOFFMAN, AND G. E. ROGERS. 1976. Wintering areas and winter ecology of White-tailed Ptarmigan in Colorado. Colorado Div. Wildl. Spec. Rep. No. 38.

BURT, W. H. 1943. Territoriality and home range concepts as applied to mammals. J. Mammal. 24:346–352.

CADE, B. S. 1985. Winter habitat preferences and migration patterns of Blue Grouse in Middle Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.

CANFIELD, R. H. 1941. Application of the line interception method in sampling range vegetation. J. For. 39:388–394.

CHOATE, T. S. 1963. Ecology and population dynamics of White-tailed Ptarmigan (*Lagopus leucurus*) in Glacier National Park, Montana. Ph.D. diss., Univ. Montana, Missoula, Montana.

DANIEL, W. W. 1978. Applied nonparametric statistics. Houghton Mifflin Company, Boston, Massachusetts.

DIXON, K. R. AND J. A. CHAPMAN. 1980. Harmonic mean measure of animal activity areas. Ecology 61:1040–1044.

ELLISON, L. 1966. Seasonal foods and chemical analysis of winter diet of Alaskan Spruce Grouse. J. Wildl. Manage. 30:729–735.

GASAWAY, W. C. 1976. Seasonal variation in diet, volatile fatty acid production and size of the cecum of Rock Ptarmigan. Comp. Biochem. and Physiol. 53A:115–121.

GIESEN, K. M. AND C. E. BRAUN. 1979a. Nesting behavior of female White-tailed Ptarmigan in Colorado. Condor 81:215–217.

——— AND ———. 1979b. Renesting of White-tailed Ptarmigan in Colorado. Condor 81: 217–218.

———, ———, AND T. A. MAY. 1980. Reproduction and nest-site selection by White-tailed Ptarmigan in Colorado. Wilson Bull. 92:188–199.

GURCHINOFF, S. AND W. L. ROBINSON. 1972. Chemical characteristics of jackpine needles selected by feeding Spruce Grouse. J. Wildl. Manage. 36:80–87.

HERZOG, P. W. 1977. Summer habitat use by White-tailed Ptarmigan in southwestern Alberta. Can. Field-Nat. 91:367–371.

———. 1980. Winter habitat use by White-tailed Ptarmigan in southwestern Alberta. Can. Field-Nat. 94:159–162.

——— AND D. A. BOAG. 1978. Dispersion and mobility in a local population of Spruce Grouse. J. Wildl. Manage. 42:853–865.

HINES, J. E. 1986. Recruitment of young in a declining population of Blue Grouse. Ph.D. thesis, Univ. Alberta, Edmonton, Alberta.

HOFFMAN, R. W. AND C. E. BRAUN. 1975. Migration of a wintering population of White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 39:485–490.

——— AND ———. 1977. Characteristics of a wintering population of White-tailed Ptarmigan in Colorado. Wilson Bull. 89:107–115.

——— AND K. M. GIESEN. 1983. Demography of an introduced population of White-tailed Ptarmigan. Can. J. Zool. 61:1758–1764.

HOFFMANN, R. S. 1961. The quality of the winter food of Blue Grouse. J. Wildl. Manage. 25:209–210.

HORWITZ, W. (ED.) 1980. Official methods of analysis of the Association of Official Analytical Chemists. Assoc. Off. Anal. Chem., Washington, D.C.

HUFF, D. E. 1970. A study of selected nutrients in browse available to the Ruffed Grouse. M.S. thesis, Univ. Minnesota, Minneapolis, Minnesota.

JENNRICH, R. I. AND F. B. TURNER. 1969. Measurement of non-circular home range. J. Theoretical Biol. 22:227–237.

JUDSON, A. 1965. The weather and climate of a high mountain pass in the Colorado Rockies. U.S. Dept. Agric., For. Serv. Res. Paper RM-16.

KOEPPL, J. W., N. A. SLADE, AND R. S. HOFFMANN. 1975. A bivariate home range model with possible application to ethological data analysis. J. Mammal. 56:81–90.

KORSHGEN, L. J. 1966. Foods and nutrition of Ruffed Grouse in Missouri. J. Wildl. Manage. 30:86–100.

MARR, J. W. 1961. Ecosystems of the east slope of the Front Range in Colorado. Univ. Colorado Studies. Ser. Biol. 8.

———, W. S. OSBURN, AND M. W. PADDOCK. 1968. Data on mountain environments. 111. Front Range, Colorado, four climax regions, 1959–1964. Univ. Colorado Studies. Ser. Biol. 28.

MAY, T. A. 1975. Physiological ecology of White-tailed Ptarmigan in Colorado. Ph.D. diss., Univ. Colorado, Boulder, Colorado.

——— AND C. E. BRAUN. 1972. Seasonal foods of adult White-tailed Ptarmigan in Colorado. J. Wildl. Manage. 36:1180–1186.

MOHR, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37:223–249.

MOSS, R. 1968. Food selection and nutrition in ptarmigan *Lagopus mutus*. Symp. Zool. Soc. London 21:207–216.

PENDERGAST, B. A. AND D. A. BOAG. 1971. Nutritional aspects of the diet of Spruce Grouse in central Alberta. Condor 73:437–443.

PULLIAINEN, E. 1978. Autumn and winter nutrition of the Capercaillie (*Tetrao urogallus*) in the northern Finnish taiga. Pp. 92–97 *in* Woodland Grouse. (T. W. I. Lovel, ed.). World Pheasant Assoc., Lamarsh Bures, Suffolk, U.K.

REMINGTON, T. E. 1983. Food selection, nutrition, and energy reserves of Sage Grouse during winter, North Park, Colorado. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.

ROBEL, R. J., J. N. BRIGGS, J. J. CEBULA, N. J. SILVY, C. E. VIERS, AND P. G. WATT. 1970. Greater Prairie Chicken ranges, movements, and habitat usage in Kansas. J. Wildl. Manage. 34:286–306.

SAS INSTITUTE, INC. 1988. SAS/STAT™ user's guide, release 6.03 edition. SAS Institute, Inc., Cary, North Carolina.

SCHMIDT, R. K., JR. 1969. Behavior of White-tailed Ptarmigan in Colorado. M.S. thesis, Colorado State Univ., Fort Collins, Colorado.

———. 1988. Behavior of White-tailed Ptarmigan during the breeding season. Pp. 270–299 *in* Adaptive strategies and population ecology of northern grouse (A. T. Bergerud and M. W. Gratson, eds.). Univ. Minnesota Press, Minneapolis, Minnesota.

SCHROEDER, M. A. AND C. E. BRAUN. 1992. Seasonal movement and habitat use by Greater Prairie-chickens in northeastern Colorado. Colorado Div. Wildl., Spec. Rep. 68.

TOEPFER, J. E. AND R. L. ENG. 1988. Winter ecology of the Greater Prairie Chicken on the Sheyenne National Grasslands, North Dakota. Pp. 32–48 *in* Prairie chickens on the Sheyenne National Grasslands (A. J. Bjugstad, Tech. Coord.). U.S. Dept. Agric., For. Serv. Gen. Tech. Rep. RM-159.

ZWICKEL, F. C. AND J. F. BENDELL. 1967. A snare for capturing blue grouse. J. Wildl. Manage. 31:202–204.