Wilson Bull., 92(3), 1980, pp. 341–351

FORAGING ECOLOGY OF PTARMIGAN AT MEADE RIVER, ALASKA

JOSEPH B. WILLIAMS, DAVE BEST AND COLLEEN WARFORD

Alaskan Willow Ptarmigan (*Lagopus lagopus*) are herbivorous birds that migrate southward in autumn through mountain passes in the Brooks Range and move northward in late winter to their principal nesting grounds on the arctic slope (Irving et al. 1967). The winter diet of this species consists principally of willow (*Salix* spp.) buds and twigs (West and Meng 1966, Weeden 1969). However, dietary patterns of ptarmigan on their major nesting grounds (tundra north of the Brooks Range) are poorly known. Therefore, this study was initiated to answer the following: (1) How do food preferences of Willow Ptarmigan vary through the summer? (2) How does habitat type influence the grazing of Willow Ptarmigan? (3) What impact does the Willow Ptarmigan have on willows?

STUDY AREA AND METHODS

Our study site was situated along the Meade River near the village of Atkasook, Alaska (70°27′N, 157°55′W). Batzli and Brown (1976) presented a description of the vegetation and soils of the area.

To ascertain the amount of time ptarmigan devote to various activities we constructed a daily activity budget (Orians 1961) by recording the behavior of birds at a signal emitted every 10 sec from an electronic metronome (Wiens et al. 1970). We categorized behavior as follows: (1) stand or crouch, (2) walk, (3) feed, (4) attack and (5) other—all other activities observed such as preening, vocalizing and flying. We timed birds during all periods of the day. To avoid bias, we followed individual birds only 5 min.

To determine diets we collected ptarmigan from tundra adjacent to our study area and stored the contents of their crops in FAA (10% formalin, 5% glacial acetic acid, 50% ethyl alcohol and 35% water). Additionally, some Eskimos gave us crops from birds they had killed. We sorted crop contents into categories, dried all material at 105°C for 24 h, then weighed each subsample. Comparison with a reference collection of plant parts allowed identification of most dietary items. Dry weights from each category from the same month were pooled for analysis. Results are expressed as percent of total dry weight for each month.

To elucidate dietary preferences in different habitat types, we erected 2 × 2-m enclosures in several habitat types (upland tundra—high center polygons, upland tundra—low center polygons, moist lake margin, streamside shrub, dry bank edge) and observed foraging by captive ptarmigan. After depriving the birds of food for 3 h, we placed them in the enclosure, allowed them to habituate to their new surroundings for 15 min and then observed (from a blind) the number of pecks on each plant species for 30 min. After approximately 1 week of captivity, birds grew accustomed to their cages and freely foraged on vegetation within them. Plant availability was determined by a stratified random sampling regime using the point frame method (Kershaw 1974). For each enclosure, we established 6 transects from a random numbers table and identified the vascular plant species closest to each point at 10 cm intervals. In 1976 two trials on each habitat type were completed using juvenile birds (ca. 250 g). In 1977 we ran 6 trials on each habitat type using an adult female (ca. 500 g).

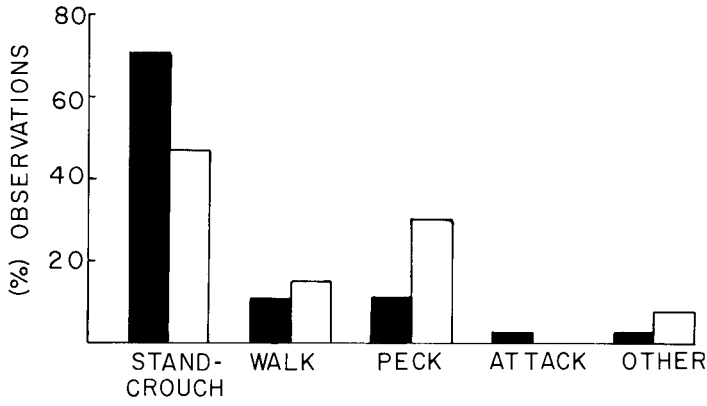

FIG. 1. The activity budget of male (shaded bars) and female (open bars) ptarmigan at Meade River, Alaska from 1–25 June 1976. N = 1620 observations for males, 715 for females. Chi-square for male vs female comparisons equals 240.8 (df = 4), $P < 0.005$.

We selected 3 habitats to examine the impact of ptarmigan on *Salix* spp. The first site was a disturbed area along the bluff of the Meade River where 5 species of willow occurred: netted willow (*Salix reticulata*), *S. pulchra*, *S. lanata*, *S. glauca* and Alaska Willow (*S. alexensis*). Except for *S. reticulata*, each species reached a height of 1 m or more. Situated along the margin of a drained lake, the second area was lower and wetter and was dominated by *S. pulchra*, although *S. reticulata* and *S. phlebophylla* were also present. Willows here were all under 0.5 m high. The third site lay along the banks of a small stream where only *S. pulchra* occurred, but it reached heights of 1 m. In August 1976, we chose twenty 1-m^2 plots for each site and constructed from hardware cloth exclosure cages over 10 of them. The cages prevented ptarmigan grazing and served as experimental plots (ungrazed); the 10 accessible plots served as controls (grazed). Each ungrazed plot and adjacent grazed plot was chosen such that the vegetation was similar in each. In mid-July of 1977, all catkins in each plot were collected, counted, dried (4 days at 65°C) and weighed. We found no evidence of other herbivores grazing on catkins on our study plots.

RESULTS

Activity budgets.—During June (1976) the activity budget of males was different from females (Fig. 1). Males often perched atop a small knoll within their territories, apparently observing their surroundings. Females spent more time feeding and walking than did males. By June 20, most females were incubating eggs, and the males became more secretive, making construction of a reliable activity budget difficult.

Composition of diet.—In June 1976, adult birds foraged on catkins and buds of *Salix* spp. (Table 1). Young *Salix* leaves (33.7%) and fruits (22.8%), and the flowers of mountain avens (*Dryas integrifolia*) comprised the major part of the diet in July. In August, *Salix* leaves and buds and the seeds of various grasses (*Luzula*, *Carex*, *Poa*) made up their diet. We

TABLE 1

A COMPARISON OF THE PERCENT DRY WEIGHT OF PLANT MATERIAL FOUND IN THE CROPS OF WILLOW PTARMIGAN ADULTS

Plant category	June N = 11		July N = 13		August N = 17	
	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops
Salix spp.						
leaves	1.7	5	33.7	12	47.2	17
buds/stems[1]	26.1	11	1.1	3	18.1	15
catkins	58.8	10	—	—	—	—
fruits	—	—	22.8	9	2.0	2
Dryas integrifolia						
flowers	—	—	21.5	5	—	—
Grasses						
seeds	—	—	0.4	1	8.0	5
Betula nana						
buds/stems	2.4	2	0.1	2	1.1	1
fruits	—	—	—	—	5.7	3
Cassiope tetragona						
flowers	—	—	5.4	7	—	—
fruits	—	—	0.7	5	7.4	6
Polygonum spp.						
flowers	—	—	2.1	2	—	—
bulbils	—	—	5.8	3	2.6	7
Eriophorum spp.						
flowers	2.5	6	—	—	—	—
Other	5.7	8	4.5	6	5.8	8
Unknown	2.8	4	1.9	6	2.1	8
Total dry wt. (g) =	18.3		8.1		9.4	

[1] Stems were usually attached to buds and undoubtedly were procured when the bud was plucked.

also obtained crops (N = 13) in August 1977 (not in Table 1). For this month we found that birds again concentrated on *Salix* buds (26%) and leaves (19%), but also took bearberry (*Arctostaphylos* spp.) fruits (32%).

In July 1976, chicks, averaging 68.2 g, often ate the leaves of *Salix* spp., but also consumed moss capsules, *Polygonum* bulbils, flowers of *D. integrifolia* and insects (Table 2). In August 1976, juvenile birds foraged on *Salix* leaves, bulbils of *Polygonum viviparum* and the seeds of grasses. We found young horsetail (*Equisetum*) sprouts in several crops. *Polygonum*

TABLE 2

A COMPARISON OF THE PERCENT DRY WEIGHT OF PLANT AND ANIMAL MATERIAL FOUND IN THE CROPS OF WILLOW PTARMIGAN CHICKS

Plant category	1976 July N = 14		1976 August N = 12		1977 July N = 17		1977 August N = 10	
	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops	% dry wt.	No. of crops
Salix spp.								
leaves	41.1	12	25.9	10	0.9	4	22.1	6
buds/stems	—	—	8.1	4	—	—	9.4	5
Polygonum spp.								
bulbils	7.6	5	10.3	9	89.3	16	0.2	3
Arctostaphylos								
fruits	—	—	3.0	4	2.4	1	20.5	4
Grasses								
seeds	0.7	1	10.3	6	—	—	19.9	4
Moss								
capsules	19.0	7	—	—	—	—	—	—
Fungi	1.1	1	—	—	+[1]	1	17.4	6
Saxifraga spp.								
bulblets	0.1	1	10.1	4	—	—	—	—
Dryas integrifolia								
flowers	0.2	1	4.5	1	—	—	—	—
fruits	8.4	3	—	—	—	—	—	—
Equisetum spp.	—	—	7.9	5	+	1	1.9	1
Cassiope tetragona								
fruits	5.1	4	3.0	3	0.3	1	—	—
Cardamine pratensis								
leaves	—	—	4.4	1	—	—	—	—
Insect gall	—	—	4.0	2	—	—	—	—
Oxytropis spp.–*Astragalus* spp.								
leaves	—	—	—	—	3.6	6	—	—
Pedicularis spp.								
leaves	3.1	2	—	—	—	—	0.3	3
fruits	—	—	3.1	3	—	—	—	—
Betula nana								
Insects	6.4	13	0.7	5	0.6	8	—	—
Other	3.7	7	1.8	5	1.3	7	5.2	6
Unknown	3.5	5	2.9	8	1.6	8	3.1	6
Total dry wt. (g)	1.2		2.4		3.7		3.2	

[1] + = values < 0.5%.

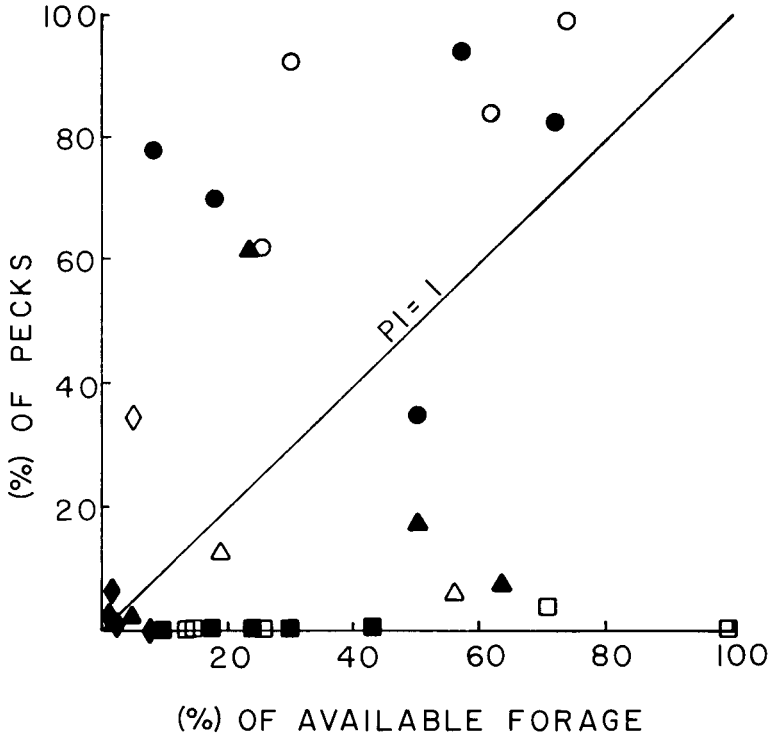

FIG. 2. Preferences of Willow Ptarmigan for monocots (squares), forbs (diamonds), deciduous shrubs (circles) and evergreen shrubs (triangles). Open symbols represent data from 1976 on juvenile birds; closed symbols represent data from 1977 on an adult female. The line represents a preference index (PI) of 1, where the proportion of pecks divided by the proportion of the plant type available equals unity. Values above the line indicate selective foraging. Statistics are in Appendix A.

bulbils dominated the diets of chicks, now averaging 73.0 g, during July 1977, much more than in 1976 (89% vs 8%), and *Arctostaphylos* berries and fungi were more important in August 1977 than in 1976 (20% vs 3% and 17% vs 0%, respectively).

Foraging trials.—For this analysis, we categorized plants consumed by ptarmigan into monocots (grasses and sedges such as *Carex aquatilis*, *Eriophorum* spp. and *Poa arctica*), forbs (herbaceous dicots such as louseworts [*Pedicularis* spp.], *Petasides frigidus* and *Polygonum* spp.), deciduous shrubs (*Salix* spp., dwarf birch [*Betula nana*] and *Arctostaphylos* spp.) and evergreen shrubs (Lapland Cassiope [*Cassiope tetragona*], Labrador tea [*Ledum palustre*] and mountain cranberry [*Vaccinium vitis-idaea*]). Results showing the percent of pecks on each plant species vs the

TABLE 3

MEAN NUMBER AND DRY WEIGHT OF *SALIX* CATKINS (±1 SE) FOUND IN PLOTS WITH AND WITHOUT PTARMIGAN GRAZING (N = 10 FOR EACH TREATMENT AT EACH LOCATION)

Location	Mean number of catkins		Mean dry weight (g)	
	Grazed	Ungrazed	Grazed	Ungrazed
Streamside	15.6 ± 4.7	85.7 ± 32.3[1]	1.1 ± 0.4	6.9 ± 2.3[1]
Disturbed area	106.1 ± 20.3	260.3 ± 48.7[1]	6.9 ± 1.4	17.4 ± 3.7[1]
Marsh margin	28.3 ± 8.3	37.8 ± 7.3	0.77 ± 0.2	0.8 ± 0.2

[1] $P < 0.05$; Wilcoxon paired sample test.

percent of each plant species available have been relegated to Appendix A.

Leaves of *Salix* and other deciduous shrubs comprised most of the diet of birds in our foraging trials (Fig. 2) (Appendix A). The adult female also selected the leaves of *D. integrifolia*, an evergreen shrub, in the dry bank habitat. Interestingly, birds avoided the leaves of evergreen shrubs such as *L. palustre*, *C. tetragona*, *Empetrum nigrum* and *V. vitis-idaea*, but readily foraged on the fruits of these species when available. Also, birds shunned the leaves of monocot grasses and when confined to pure patches of *C. aquatilis*, they did not feed.

Exclosure experiments.—Ptarmigan grazing appeared to affect the production of *Salix* catkins in 2 of the 3 habitats that we tested (Table 3; Wilcoxon paired sample test, $P < 0.05$). Where willow shrubs were more arborescent (streamside and disturbed area), we found catkin numbers to be significantly reduced in the grazed plots. But in the lake margin habitat, where *Salix pulchra* is somewhat decumbent, we found no significant differences between ungrazed and grazed plots. Thus, the impact of ptarmigan foraging on willows appears greater in habitats with taller willows, which would be above the snow earlier in spring and later in autumn.

DISCUSSION

Activity budgets for birds during June indicated that males spent a considerable amount of time in territorial surveillance and that females foraged more than males prior to nesting (Fig. 1). West (1968) showed that female Willow Ptarmigan required significantly more energy during late spring than any other time period. Moss (1972, 1977) thought female Red Grouse (*L. l. scoticus*) selected foods because of high nutrient content rather than for energy in the spring. The greater time spent foraging by females suggests that they were meeting increased physiological demands for either nutrients or energy, or both.

The diet of Alaskan Willow Ptarmigan during winter has been well documented and is composed principally of *Salix* buds and twigs (Bent 1932, West and Meng 1966, Weeden 1969). However, only 1 previous study has been done on their summer diet on the North Slope. From 23 crops collected at Umiat during June–August, West and Meng (1966) reported *Salix* leaves and *Equisetum* were the main constituents of the diet of this species (42.9% and 15.7% by dry weight, respectively). Since they lumped data for the 3 months, seasonal changes could not be determined. At Meade River birds concentrated their foraging on *Salix* catkins in June. We interpret this use of catkins as indicative that they are relatively high in nutritional value at this time. West and Meng (1966) found a marked increase of energy content in catkin buds of *Salix* just prior to flowering. Chapin et al. (unpubl.) found that the concentration of nitrogen and phosphorous of *Salix* catkins at Meade River reached a peak in mid-June and dropped linearly through the summer. In July, adults foraged more on young *Salix* leaves and maturing seed capsules. *Salix* leaves in July have a caloric value similar to wintering buds (West and Meng 1966), but the concentration of nitrogen and phosphorous in *Salix* leaves is highest at this time (Chapin et al., unpubl.). The lack of *Salix* buds in diets of ptarmigan in July may be because buds are relatively low in caloric content at this time (West and Meng 1966), or because buds are small and developing during July.

Because early June 1977 was relatively warm at Meade River (4.4°C mean temperature vs 2.7°C in 1976), plants were phenologically advanced by about 2 weeks, compared to the previous summer. Ptarmigan diets for August 1977 showed *Arcostaphylos* berries were favored, although *Salix* leaves and buds were still important. *Arctostaphylos* berries were still small and green when we left in mid-August 1976. We suspect that during September of normal years berries become important in ptarmigan diets because they are a readily available source of carbohydrates and nutrients (Gardarsson and Moss 1970, Moss and Parkinson 1975), and because *Salix* leaves have lost much of their nitrogen and phosphorous by translocation by this time (Chapin et al., unpubl.).

Chicks of gallinaceous birds often rely on arthropods as an important source of food (Ford et al. 1938, Christiansen and Kraft 1953, Pendergast and Boag 1970). Bent (1932) wrote that Willow Ptarmigan chicks are primarily insectivorous, but more recent studies indicate that insects comprise only 5–30% of the diets of ptarmigan chicks (Weeden 1969, Gardarsson and Moss 1970, Savory 1977). In this study chicks used a wide variety of flowers, fruits and seeds in addition to willow leaves in July 1976, but concentrated almost entirely on *Polygonum* bulbils during July 1977. We collected insufficient data to compare diets of very young chicks with older ones in July to see if young chicks concentrated more on insects.

But crops of 6 young chicks (<30 g) that we collected all contained more plant material than insects and never exclusively insects. Food items taken early in life by chicks (fruits, seeds, moss capsules) may be more digestible and/or more nutritious than *Salix* leaves, thus chicks would be able to obtain more energy and nutrients from them (Savory 1977). Gardarsson and Moss (1970) reported that *P. viviparum* spikes and bulbils comprised 62% of the diets of Icelandic ptarmigan chicks and that these foods were relatively high in nitrogen and phosphorus. Additionally, they found that bulbils were more easily digested (in vitro digestibility) than leafy materials. Moss and Parkinson (1975), using captive adult Rock Ptarmigan (*L. mutus*), ascertained that bulbils of *P. viviparum* were a good source of metabolizable energy, protein and phosphorus. Hence, this diet may provide juveniles with more needed protein for growth than would leaves. As chicks mature, their cecal flora probably develops, making leaves more digestible, and they begin to eat the leaves of *Salix* and other plants (McBee and West 1969, Gassaway et al. 1975). Part of the difference in chick diets between years perhaps can be attributed to the fact that 1977 was a warmer summer and thus seed and bulbil development was earlier.

Our grazing experiments documented the strong preference of Willow Ptarmigan for the leaves of deciduous shrubs, especially *Salix*, in all habitat types at Meade River. Batzli (unpubl.) found that leaves of *S. pulchra* and other *Salix* species contain tannins which are secondary metabolic products found in plants that form complexes with proteins rendering them indigestible (Feeny 1970). Apparently Willow Ptarmigan have evolved a mechanism which makes this line of defense in *Salix* ineffective.

Ptarmigan avoided the leaves of most evergreen shrubs (*C. tetragona*, *E. nigrum*, *L. palustre*), but did forage on the leaves of *D. integrifolia* in the dry bank edge habitat. Batzli (unpubl.) found that microtine rodents at Meade River (brown lemming [*Lemmus trimucronatus*], Greenland collared lemming [*Dicrostonyx groenlandicus*] and tundra vole [*Microtus oeconomus*]) also did not eat leaves of any evergreen shrubs except *Dryas*. Moreover, he showed that the leaves of evergreen shrubs contained a greater variety of chemical defenses (tannins, alkaloids, anthraquinones) than monocots, forbs, or deciduous shrubs. That leaves of evergreen shrubs at Meade River are highly protected by secondary metabolic products conforms to the suggestion of Rhoades and Cates (1976) that the most highly defended leaf tissue in plants should be the mature leaves of long-lived, common, evergreen, climax woody perennials.

SUMMARY

On a study area near Atkasook, Alaska, in the early summer, male Willow Ptarmigan spent more time in apparent territory surveillance, while females foraged more, possibly to meet the increased physiological demands of egg-laying. Diets of adult birds consisted pri-

marily of *Salix* catkins and buds in June, of young *Salix* leaves and maturing fruits in July, and of *Salix* leaves and buds, and the seeds of grasses in August. In addition to *Salix* leaves, chicks foraged on fruits, flowers and various insects. Foraging trials in various habitat types demonstrated the strong preference of Willow Ptarmigan for *Salix* leaves, and showed that these birds avoided the leaves of certain evergreen shrubs, perhaps because they possess chemical defenses. With exclosure experiments, we showed that ptarmigan reduce catkin numbers more along streams where willows are more aborescent.

ACKNOWLEDGMENTS

This study is part of the Research on Arctic Tundra Environments (RATE) program sponsored by the National Science Foundation. We wish to express appreciation to Dr. Steve McLean and his group for help with the ptarmigan exclosure experiments. Drs. George Batzli, Don Spailing and John Roseberry made helpful comments on an earlier draft.

LITERATURE CITED

BATZLI, G. O. AND J. BROWN. 1976. Research on arctic tundra environments (RATE). The influence of grazing on arctic tundra ecosystems. Arctic Bull. 2:153–160.

BENT, A. C. 1932. Life histories of North American gallinaceous birds. U.S. Natl. Mus. Bull. 162.

CHRISTIANSEN, B. AND A. KRAFT. 1953. Lirypekyllingenes naering. The food of Willow Grouse chicks. Norges Jeger-og Fisker-Forbunds Tidsskrift. Nr. 4. Cited in Peters, S. S. 1958. Food habits of Newfoundland Willow Ptarmigan. J. Wildl. Manage. 22:384–394.

FEENY, P. 1970. Seasonal changes in oak leaf tannins and nutrients as a cause of spring feeding by winter moth caterpillars. Ecology 51:565–581.

FORD, J., H. CHITTY AND A. D. MIDDLETON. 1938. The food of partridge chicks (*Perdix perdix*) in Great Britain. J. Anim. Ecol. 7:251–265.

GARDARSSON, A. AND R. MOSS. 1970. Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. Pp. 47–71 *in* Animal populations in relation to their food resources, (A. Watson, ed.). Oxford Univ. Press, Oxford, England.

GASSAWAY, W. C., D. HOLLEMAN AND R. G. WHITE. 1975. Flow of digesta in the intestine and cecum of the Rock Ptarmigan. Condor 77:467–474.

IRVING, L., G. C. WEST, L. J. PAYTON AND S. PANEAK. 1967. Migration of Willow Ptarmigan in Arctic Alaska. Arctic 20:77–85.

KERSHAW, K. A. 1974. Quantitative and dynamic plant ecology. American Elsevier Pub. Co., New York, New York.

MCBEE, R. H. AND G. C. WEST. 1969. Cecal fermentation in the Willow Ptarmigan. Condor 71:54–58.

MOSS, R. 1972. Food selection by Red Grouse (*Lagopus lagopus scoticus*) in relation to chemical composition. J. Anim. Ecol. 41:411–428.

———. 1977. The digestion of heather by Red Grouse during spring. Condor 79:471–477.

——— AND J. A. PARKINSON. 1975. The digestion of bulbils (*Polygonum viviparum*) and berries (*Vaccinium myrtillus* and *Empetrum* sp.) by captive ptarmigan (*Lagopus mutus*). Br. J. Nutr. 33:197–206.

ORIANS, G. 1961. The ecology of Blackbird (Agelaius) social systems. Ecol. Monogr. 31:285–312.

PENDERGAST, B. A. AND D. A. BOAG. 1970. Seasonal changes in diet of Spruce Grouse in central Alberta. J. Wildl. Manage. 34:605–611.

RHOADES, D. F. AND R. G. CATES. 1976. Toward a general theory of plant antiherbivore chemistry. Pp. 168–213 *in* Biochemical interactions between plants and insects, (J. W. Wallace and R. L. Mansell, eds.). Plenum Press, New York, New York.

SAVORY, C. J. 1977. The food of Red Grouse chicks *Lagopus l. scoticus*. Ibis 119:1–9.

WEEDEN, R. B. 1969. Foods of Rock and Willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86:271–281.

WEST, G. C. 1968. Bioenergetics of captive Willow Ptarmigan under natural conditions. Ecology 49:1035–1045.

——— AND M. S. MENG. 1966. Nutrition of Willow Ptarmigan in northern Alaska. Auk 83:603–615.

WIENS, J. A., S. C. MARTIN, W. R. HOLTHAUS AND F. A. IWEN. 1970. Metronome timing in behavioral ecology studies. Ecology 51:350–352.

NATURAL SCIENCE DEPT., PEPPERDINE UNIV., MALIBU, CALIFORNIA 90265 (JBW, CW) AND WILDLIFE ECOLOGY, UNIV. WISCONSIN, MADISON, WISCONSIN 53706 (DB). (PRESENT ADDRESS JBW: DEPT. BIOLOGY, JOSEPH LEIDY LABORATORY OF BIOLOGY G7, UNIV. PENNSYLVANIA, PHILADELPHIA, PENNSYLVANIA 19104.) ACCEPTED 25 JUNE 1979.

APPENDIX A

PLANT AVAILABILITY (% COVER) AND THE PERCENTAGE OF OBSERVED PECKS BY PTARMIGAN ON THE PLANT SPECIES WITHIN 2 × 2 M PENS PLACED IN VARIOUS HABITAT TYPES[1]

1976			1977		
Plant species	Availability	% pecks	Plant species	Availability	% pecks
		Upland tundra—P_L			
Carex aquatilis	99.0	—	*Ledum palustre*	28.0	—
Eriophorum spp.	1.0	—	*Carex aquatilis*	22.3	—
		0	*Vaccinium vitis-idaea*	19.0	16.7
			Salix pulchra	15.0	49.0
			Eriophorum spp.	6.8	—
			Salix phlebophylla	3.7	21.0
			Cassiope tetragona	2.6	1.5
			Other	6.0	11.5
					(2863)[2]
		Upland tundra—P_H			
Ledum palustre	30.0	—	*Vaccinium vitis-idaea*	34.8	8.8
Salix phlebophylla	29.2	92.3	*Ledum palustre*	29.0	0.1
Carex bigelowii	13.2	—	*Eriophorum vaginatum*	11.6	—
Vaccinium vitis-idaea	10.6	—	*Carex bigelowii*	10.0	—
Diapensia lapponica	8.8	—	*Rubus chameamorus*	3.5	—
Cassiope tetragona	7.0	5.6	*Salix phlebophylla*	3.0	—
Eriophorum vaginatum	0.8	—	*Salix pulchra*	2.5	55.1
Pedicularis capitata	—	—	*Betula nana*	2.0	2.4
		(551)	*Poa arctica*	1.5	—
			Other	1.5	12.6
					(2666)

APPENDIX A

CONTINUED

1976			1977		
Plant species	Availability	% pecks	Plant species	Availability	% pecks
		Moist lake margin			
Carex aquatilis	69.5	3.6	*Salix pulchra*	56.5	94.0
Salix pulchra	25.0	61.0	*Carex aquatilis*	37.0	—
Pedicularis sudetica	3.2	35.3	*Eriophorum* spp.	4.0	—
Caltha sp.	2.1	—	*Polygonum viviparum*	1.1	6.0
		(1097)	Other	1.0	—
					(1700)
		Streamside shrub			
Salix pulchra	58.3	90.8	*Salix pulchra*	63.0	74.7
Carex spp.	23.4	—	*Betula nana*	9.0	7.7
Betula nana	15.9	9.0	*Petasides frigidus*	5.5	0.1
Calamagrostis holmii	1.5	—	*Calamagrostis holmii*	5.0	0.2
Petasides frigidus	0.7	—	*Carex* spp.	4.5	0.1
		(503)	*Vaccinium vitis-idaea*	4.5	3.8
			Pyrola grandifolia	3.0	—
			Other	4.0	13.4
					(1941)
		Dry bank edge			
Arctostaphylos sp.	53.1	21.5	*Arctostaphylos* sp.	38.3	11.8
Dryas integrifolia	17.4	13.0	*Dryas integrifolia*	22.7	62.2
Carex spp.	14.2	—	*Carex* spp.	15.6	—
Salix phlebophylla	9.5	62.5	*Salix phlebophylla*	11.6	23.2
Artemesia sp.	2.3	—	*Eriophorum vaginatum*	2.5	—
Diapensia lapponica	1.5	—	*Artemesia* sp.	1.5	0.2
Other	2.0	2.7	*Cassiope tetragona*	1.5	—
		(752)	*Salix pulchra*	1.0	0.1
			Polygonum bistorta	1.0	0.7
			Stellaria laeta	1.0	—
			Other	3.0	1.8
					(8717)

[1] Chi-square values for 1976 equal 100 (df = 1), 507.5 (df = 7), 1134.7 (df = 3), 534.8 (df = 4), 69.8 (df = 6) for upland tundra—low center polygons (P_L), upland tundra—high center polygons (P_H), moist lake margin, streamside shrub, and dry bank edge, respectively. In 1977 for the adult female, Chi-square values equal 2551.1 (df = 7), 3759.7 (df = 9), 1494.6 (df = 3), 446.2 (df = 7), and 5138.3 (df = 10) for the same sequence of habitats. $P < 0.005$ in all cases.

[2] Numbers in parentheses equal the total number of observed pecks.