NUTRITION OF WILLOW PTARMIGAN IN NORTHERN ALASKA[1]

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THE arctic and subarctic regions of Alaska and northern Canada are extensive areas occupied by large populations of relatively few species of animals. Many of these are browsers, such as moose (*Alces alces*), porcupine (*Erethizon dorsatum*), snowshoe hare (*Lepus americanus*), tundra hare (*L. othus*), and two species of Ptarmigan, Rock (*Lagopus mutus*), and Willow (*L. lagopus*). These species obtain most of their nutrition from the stems, bark, twigs, buds, and leaves of brushy plants and trees. Beyond the limit of trees, however, only a few genera of bushy plants are available, the most abundant being *Salix* (willow), *Alnus* (alder), and *Betula* (birch). *Salix* appears to be the most important genus and sustains Willow Ptarmigan and moose throughout the winter in the arctic slope area of northern Alaska. Willow Ptarmigan have perhaps a more specialized and uniform diet than any other northern animal since during many winter months up to 94 per cent of their diet consists of buds and twigs of willow, and 80 per cent of this may be of a single species. The adaptation of the ptarmigan's own digestive enzymes and the ability of its intestinal and cecal microflora to provide nutritive and energy requirements to the bird from a single generic plant source is unusual and interesting. This paper reports on the results of one of a series of studies which has been undertaken to understand these adaptations and to document seasonal and latitudinal variations in the diet of these birds.

The population we studied breeds in the valley of the Colville River, north of the Brooks Range in northern Alaska and migrates south through passes in the mountains to winter throughout the river valleys of the range as far south as the Koyukuk River, a northern tributary of the Yukon. This population has been under observation since 1948 by Laurence Irving and Simon Paneak who have recorded changes in seasonal abundance and movements in several papers (Irving and Paneak, 1954; Irving, 1960; Irving *et al.*, 1965). The population segregates into age and sex groups in its migration south in the fall and these groups become distributed along a north-south gradient through the Brooks Range (Irving *et. al.*, 1965).

Samples from ptarmigan flocks were collected as often as possible from Umiat (69° 24′ N lat., 152° 07′ W long.), Anaktuvuk Pass (68° 09′ N, 151° 46′ W), Crevice Creek (67° 22′ N, 152° 04′ W), and Bettles Field (66° 55′ N, 151° 28′ W) (Figure 1). Details on sex composition of the

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migrating population and on weight and mensural characteristics of the birds are reported elsewhere (Irving *et al.*, 1967*a*; West *et al.*, MS).

METHODS

The crops of 540 birds were examined. Crops were removed and weighed to the nearest tenth of a gram on a triple beam balance. The crop membrane was opened and the contents scraped into a tin cup for preliminary air drying. The crop membrane was immediately weighed, so that the weight of the crop contents could be obtained. Each crop sample was sorted into component species, by comparison with a reference collection. (Since the taxonomy of willows is uncertain, and some workers think hybridization between willow species occurs, some error in identification undoubtedly exists.) The samples were then thoroughly dried at 80–90°C, and weighed to the nearest one-hundredth of a gram on a Mettler analytical balance. All results

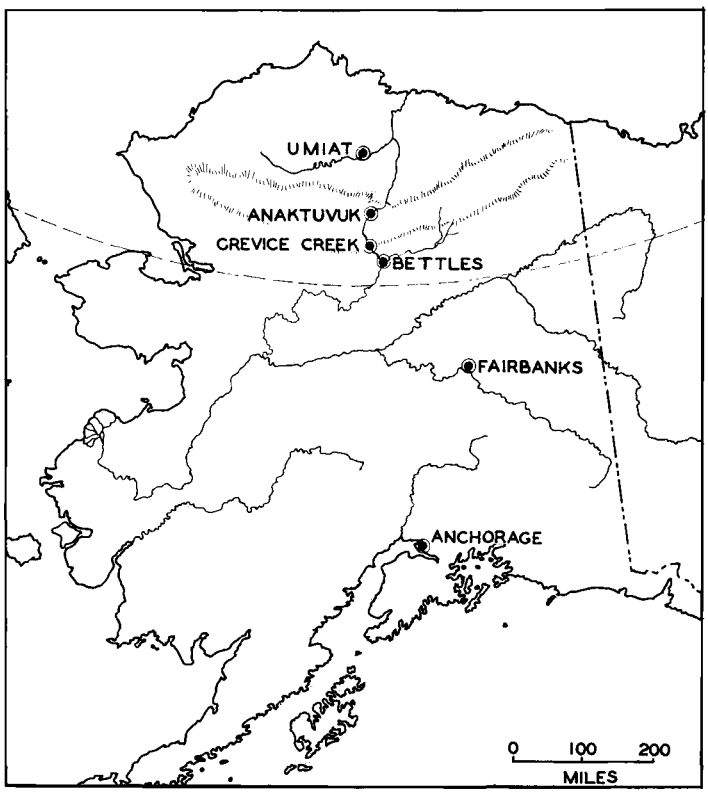

Figure 1. Sampling locations in the Brooks Range of northern Alaska. Umiat is on the Colville River. Anaktuvuk is at the summit of the Brooks Range at the pass between the Anaktuvuk River, which flows north, and the John River, which flows south. Crevice Creek is on the John River. Bettles is on the Koyukuk River, a tributary of the Yukon. The arctic circle is indicated by the dashed latitude line.

are expressed in terms of per cent by dry weight. Samples of each species of plant were then combined into groups by month and ground to a powder in a Wiley mill. From one to six samples, depending on the amount available, were taken from the powdered sample, and the caloric values determined in a Parr adiabatic oxygen bomb calorimeter. Duplicate samples gave a variation of less than two per cent in all cases.

TABLE 1

ANALYSIS OF CONTENTS OF WILLOW PTARMIGAN CROPS

	Umiat			*Anaktuvuk*			*Crevice Creek*			*Bettles*		
	N	*Average dry weight (g)*	*Per cent water*	*N*	*Average dry weight (g)*	*Per cent water*	*N*	*Average dry weight (g)*	*Per cent water*	*N*	*Average dry weight (g)*	*Per cent water*
September	7	5.39	78.7									
October	48	4.95	54.0	41	9.03	58.7						
November	3	0.84	62.4							27	9.12	55.9
December				20	7.34	60.8						
January				6	31.19	56.7				12	8.93	54.4
February				19	11.52	62.6	32	7.46	53.6	5	14.66	47.6
March	31	12.10	58.5	18	6.54	58.5	16	14.11	50.1	8	4.29	52.9
April	24	6.13	61.2	18	4.56	61.1	17	4.92	56.6			
May	55	3.87	62.1	130	3.95	57.6						
June through August	23	1.29	78.1									

TABLE 2

AVERAGE CONTENTS OF CROPS OF WILLOW PTARMIGAN AT UMIAT

Species	*Plant part*[1]	*Per cent of dry weight*						
		September	*October*	*November*	*March*	*April*	*May*	*June through August*
Salix alaxensis	Bu, T	1.75		47.90	57.88	76.52	40.37	3.63
S. glauca	Bu, T	17.73	33.16	11.67	0.02	0.18	2.82	
S. pulchra	Bu, T	1.06	24.33	29.84	1.53	2.06	4.92	0.02
S. richardsonii	Bu, T		15.06		6.53	0.90	12.16	
S. arbusculoides	Bu, T	8.96	4.20	2.86	31.75	16.17	33.84	
Salix spp.	L							42.98
Salix spp.	C							0.80
Betula glandulosa	Bu, T	7.51	4.31	1.20	1.65	2.94	0.70	0.03
B. glandulosa	C	9.08	4.73	0.14	0.02	0.12	0.15	4.80
Dryas integrifolia	L	1.56	3.50	6.37		0.44	0.04	
Equisetum scirpoides	St	2.64	0.21					15.71
Vaccinium vitis-idea	L					0.52	1.43	5.01
V. uliginosum	Be	41.80	8.10					4.85
V. uliginosum	Bu, T	7.16	1.64					0.23
Arctostaphylos uva-ursi	Be							8.42
Miscellaneous[2]	—	0.75	0.76	0.62	0.62	0.25	0.67	13.22

[1] Be = berries, Bu = buds, C = catkins, F = flowers, L = leaves, St = stems, T = twigs.

[2] Includes items not represented by over five per cent in any month. Seeds of *B. glandulosa, Carex, Pedicularis, Papaver,* and *Astralagus*; leaves of *B. glandulosa, V. uliginosum,* and *Poa arctica*; buds and catkins of *Alnus crispa*; berries of *V. vitis-idea*; and flowers of *Eriophorum angustifolium* were represented. A spider was found in one crop and a snail (*Succinea*) in another.

TABLE 3
AVERAGE CONTENTS OF CROPS OF WILLOW PTARMIGAN AT ANAKTUVUK

Species	*Plant part*[1]	*Per cent of dry weight*						
		October	*December*	*January*	*February*	*March*	*April*	*May*
Salix alaxensis	Bu, T	0.44	24.86	47.57	80.95	74.15	72.47	24.58
S. glauca	Bu, T	37.80	4.04	0.48	1.51	4.50	0.85	20.09
S. pulchra	Bu, T	15.33	5.64	0.10	0.04	0.02	2.69	17.37
S. richardsonii	Bu, T	27.90	49.91	41.10	14.74	14.91		4.52
S. arbusculoides	Bu, T	2.88	10.90	7.58	2.71	5.92	12.28	3.48
Betula glandulosa	Bu, T	5.47	1.32	2.63	0.05	0.50	6.48	8.32
B. glandulosa	C	6.29	3.33	0.53			0.63	1.28
Dryas integrifolia	L	2.49					4.09	12.51
D. octopetala	L	0.07					0.31	6.47
Miscellaneous[2]	—	1.32		0.01			0.20	1.38

[1] See Table 2 for key.

[2] Includes items not represented by over five per cent in any month. Stems of *Equisetum scirpoides*; seeds of *Hedysarum alpinum*; bulbils of *Polygonum viviparum*; leaves of *Vaccinium vitis-idea*, *Empetrum nigrum*, *Poa arctica*, and *Polytrichum*; buds and catkins of *Alnus crispa*; and flowers of *Eriophorum angustifolium* were represented.

RESULTS AND DISCUSSION

Average dry weights of crop contents increased from fall through winter and decreased again reaching a low in summer (Table 1). Since the amount of daylight available during the winter is limited to only a few hours, especially during December and January, it is likely that the birds fill their crops when it is light and digest when it is dark. During summer, it is light throughout the 24-hour day and birds do not fill their crops, but rather appear to eat at more regular intervals (Irving *et al.*, 1967*b*).

Water content of foods eaten remains rather stable at 50–60 per cent during the winter but increases during summer and early fall, as a result of the inclusion of large amounts of berries in the diet (Tables 1, 2, and 3).

Availability of plants.—The availability of different plant species to ptarmigan is affected primarily by the height of the plants and the amount of snow cover in different localities. Although no quantitative survey has been made, the same species of plants used in the diet are available, in varying concentrations, throughout the Brooks Range with the exception of aspen (*Populus tremuloides*) and hybrid birch (*Betula glandulosa* × *B. papyrifera?*) which occur only in the southern part of the range.

Salix alaxensis is a tall shrub reaching 15 to 20 feet throughout the Brooks Range, and *S. glauca, S. pulchra,* and *S. richardsonii* are shorter, rarely exceeding 4 feet, and commonly being less than 2 feet at Umiat and Anaktuvuk. *S. arbusculoides* is of a medium height, reaching 6 feet at Umiat and Anaktuvuk and up to 10 feet at Bettles.

Snow cover varies annually, but accumulates to a greater depth at

TABLE 4
AVERAGE CONTENTS OF CROPS OF WILLOW PTARMIGAN AT CREVICE CREEK

Species	*Plant part*[1]	*Per cent of dry weight*		
		February	*March*	*April*
Salix alaxensis	Bu, T	6.48	1.85	5.88
S. glauca	Bu, T	10.83	16.87	9.02
S. pulchra	Bu, T	24.49	22.08	48.11
S. richardsonii	Bu, T	18.27	11.49	2.27
S. arbusculoides	Bu, T	15.47	31.31	15.98
Betula glandulosa	Bu, T	7.90	6.77	10.18
B. glandulosa	C	13.54	9.12	8.58
Miscellaneous[2]	—	3.02	2.62	0.52

[1] See Table 2 for key.

[2] Includes items not represented by over five per cent in any month. Buds and twigs of *Populus tremuloides* and *B. glandulosa* × *B. papyrifera* (?) were represented.

Bettles and Crevice Creek than farther north probably because of the lack of wind in the forested area along the southern slope of the Brooks Range. At Umiat, winds are frequent and the area is flat. Snow rarely accumulates deeper than three feet on the level. However, this is sufficient to cover *S. glauca, S. richardsonii,* and *Betula glandulosa,* and most of the branches of *S. pulchra* and *S. arbusculoides.* Winds through Anaktuvuk are often strong and frequent enough to make many areas practically bare of snow leaving some of the shorter species of willow and dwarf birch available. Accumulation of snow in stands of *S. alaxensis* regularly reaches four feet leaving only some *S. arbusculoides* available but *S. alaxensis* projects several feet above the snow line even in the worst winters. The presence of hoar frost on willow branches at Anaktuvuk which occurs during fall discourages ptarmigan from eating buds, and birds may not feed until

TABLE 5
AVERAGE CONTENTS OF CROPS OF WILLOW PTARMIGAN AT BETTLES

Species	*Plant part*[1]	*Per cent of dry weight*			
		November	*January*	*February*	*March*
Salix glauca	Bu, T	11.90	4.00	8.34	11.94
S. pulchra	Bu, T	28.45	32.23	32.57	18.21
S. richardsonii	Bu, T	5.43	4.55	2.87	0.57
S. arbusculoides	Bu, T	9.82	10.59	21.31	27.30
Betula glandulosa	Bu, T	3.74	2.65	1.89	6.04
B. glandulosa	C	17.63	20.94	30.82	33.39
Populus tremuloides	Bu, T	19.86	24.41	1.78	2.55
Miscellaneous[2]	—	3.17	0.63	0.42	

[1] See Table 2 for key.

[2] Includes items not represented by over five per cent in any month. Stems of *Equisetum variegatum*; leaves of *Dryas integrifolia, Vaccinium vitis-idea,* and *V. uliginosum*; and buds and twigs of *B. glandulosa* × *B. papyrifera* (?) were represented.

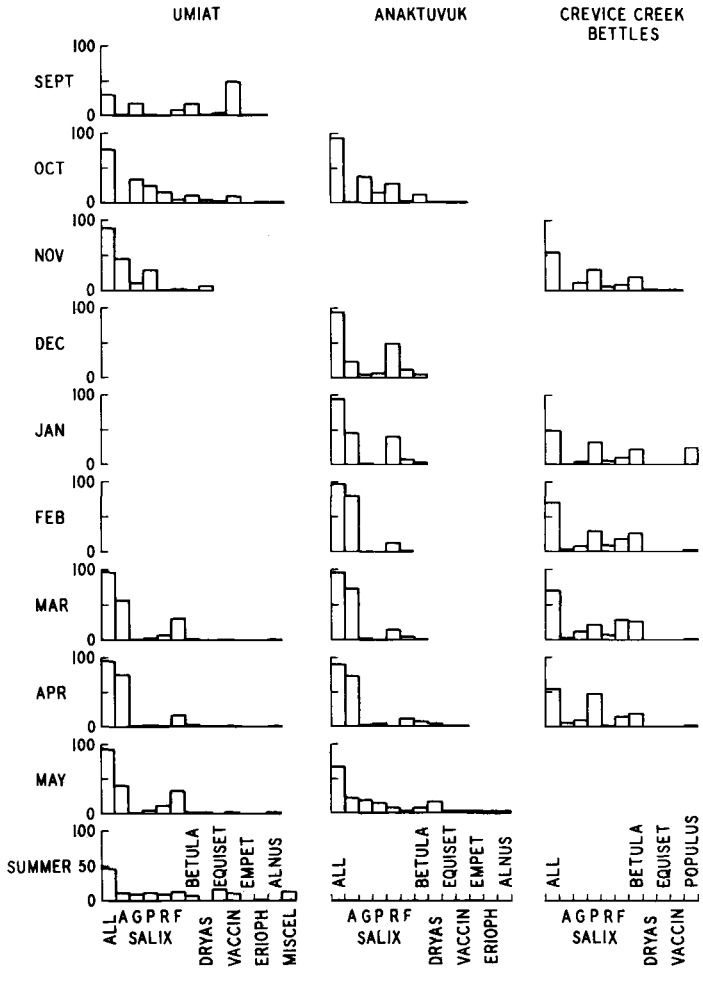

Figure 2. Summary of diets of Willow Ptarmigan. The limited data from Bettles and Crevice Creek have been averaged. The vertical scale is in per cent composition of dry weight. Summer includes June, July, and August. Plant groups are as follows: *Salix* All = all species of willow combined, A = *S. alaxensis*, G = *S. glauca*, P = *S. pulchra*, R = *S. richardsonii*, F = *S. arbusculoides*, *Betula* = *B. glandulosa* and *B. glandulosa* × *B. papyrifera*(?), *Dryas* = *D. integrifolia* and *D. octopetala*, Equiset = *Equisetum scirpoides* and two other undetermined species, Vaccin = *Vaccinium uliginosum* and *V. vitis-idea*, Empet = *Empetrum nigrum*, Erioph = *Eriophorum angustifolium*, Alnus = *A. crispa*, Populus = *P. tremuloides*, Miscel = All other dietary components (see Tables 2–5).

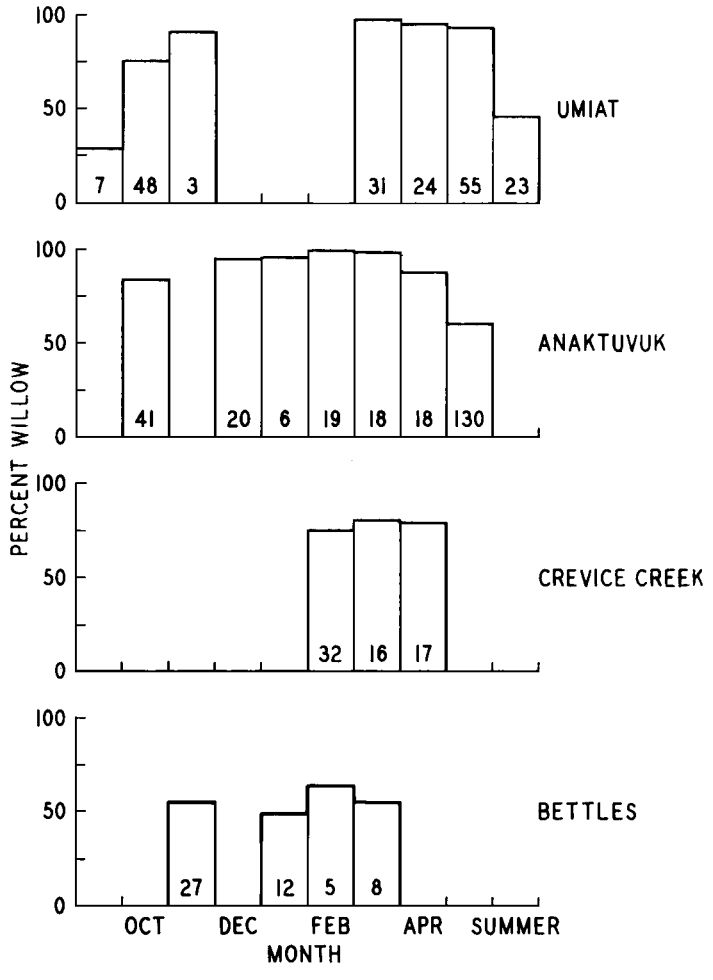

Figure 3. Percentage of the diet of Willow Ptarmigan that consists of willow buds, twigs, and leaves. Per cent composition is of dry weight. Numbers in the bars indicate the number of crops sampled.

later in the day when the sun or wind has dissipated the frost (Simon Paneak, pers. comm.). Snow accumulates regularly to four feet in Bettles, but all species of willow as well as dwarf and hybrid birch and aspen are still available above the snow, since they grow to greater heights in this more southerly locality.

Alder (*Alnus crispa*) is abundant in certain areas in the Brooks Range. However, it is seldom used by Willow Ptarmigan, perhaps because of its chemical composition. It is high in fat content (West and Meng, MS) and

its caloric content is high, but it is unpleasant to human taste and may be unpalatable to these birds.

Use of plants.—The average diets for each sampling period and location are listed in Tables 2 through 5, and summarized in Figure 2. The total amount of willow used during the winter is less in samples collected in the southern part of the wintering range (Figure 3), while the amount of birch and aspen increases there. Fall, late spring, and summer diets contain a greater variety of items than do those in winter (Tables 2–5, Figure 2), because of the greater availability of plants. There is a gradual increase in use of willow as snow covers herbaceous plants and as winter progresses, but as the snow melts, birds again use other genera (Figure 2). It is interesting to note that adults consumed little animal food at any time, but we do not know if insects play any role in the diet of chicks during the summer at Umiat, or if adults take animal food during years of high insect abundance.

An obvious shift in dependence by birds on the different species of willow, evident in Figure 2, is related to the amount of snow cover and height of the bushes. *Salix alaxensis* is used very little in the fall, but gradually increases in the diet through winter at Umiat and Anaktuvuk. As snow covers the shorter species, the birds are forced up into the taller *S. alaxensis* where they often perch precariously, nipping off the buds and terminal twigs. The dependence on this species increases until from 58 to 80 per cent of the total diet consists of *S. alaxensis* at Umiat and Anaktuvuk (Tables 2 and 3). At Crevice Creek and Bettles, however, the birds do not depend on *S. alaxensis* (not found in any crops from Bettles) since other species are readily available above the snow (Tables 4 and 5). Therefore the diet at the two southern localities has a much more diversified species composition throughout the winter (Figure 2).

At Umiat and Anaktuvuk, preference during the fall and early winter seems to be for the shorter species (*S. glauca, S. richardsonii,* and *S. pulchra*); during the spring, *S. arbusculoides* is eaten with greater frequency than before. This may be because the last species is slightly taller and has a good crop of buds since they were not eaten during the fall. At Bettles and Crevice Creek, the birds appear to prefer *S. pulchra* throughout the winter and also supplement their diet liberally with birch and occasionally aspen (Figure 2).

Caloric content of the diet.—Caloric values were separately determined on whole samples of buds, twigs, leaves, etc. of each plant (Table 6). Samples from the four localities were pooled since there proved to be no significant differences in caloric values among localities. Amounts of ash were not taken into account in the calculations. It was evident, however, from the ash remaining in the combustion capsule after ignition that the

TABLE 6
CALORIC EQUIVALENTS OF FOODS EATEN BY WILLOW PTARMIGAN

Species	*Plant part*[1]	*calories/gram dry weight*[2]				
		September October November	*December January February*	*March April*	*May Early June*	*July August*
Salix alaxensis	Bu	4646(4)	4799(3)	4802(12)	4836(6)	4471(3)
S. alaxensis	T	4927(3)	—	—	—	—
S. glauca	Bu	5168(1)	—	5018(7)	4883(3)	—
S. glauca	T	5173(9)	—	—	4885(2)	—
S. pulchra	Bu	4961(9)	4959(6)	4877(9)	4837(9)	4671(3)
S. pulchra	T	5118(4)	—	—	4909(2)	—
S. richardsonii	Bu	4890(9)	4866(2)	4905(11)	4941(6)	—
S. arbusculoides	Bu	5268(3)	5080(3)	5024(10)	5039(4)	—
S. arbusculoides	T	—	—	5005(5)	5016(3)	—
Salix spp.	L	—	—	—	—	4670(15)
Betula glandulosa	Bu, T	5922(9)	5656(6)	5655(14)	5609(2)	—
B. glandulosa	C	5505(7)	5497(6)	5391(9)	5269(3)	5199(3)
Dryas integrifolia	L	4923(6)	—	4890(5)	4877(3)	—
D. octopetala	L	4933(1)	—	—	4886(3)	—
Vaccinium vitis-idea	Be	—	—	—	4516(3)	—
V. vitis-idea	L	4999(3)	—	4874(2)	4771(2)	—
V. uliginosum	Be	4833(3)	—	—	—	4550(6)
Populus tremuloides	Bu	5266(2)	5421(1)	5633(5)	—	—
Alnus crispa	Bu	5626(2)	—	5504(4)	—	5394(3)
A. crispa	C	—	—	—	5176(1)	—
Equisetum scirpoides	Whole plant	4114(3)	—	—	—	—

[1] See Table 2 for key.

[2] Sample size in parentheses.

amount of ash was rather constant for all samples except *Equisetum* which showed large amounts of silica, therefore reducing its caloric value per gram dry weight. Birch, alder, and aspen have consistently higher caloric values than willow or other shrubby or herbaceous plants because of their higher lipid content (West and Meng, MS). This correlation has been pointed out recently by Bliss (1962) for alpine species. There are apparent differences in caloric value between different plant parts at any one season. For example *Betula glandulosa* buds and twigs in fall and again in spring have higher values than do the catkins (Figure 4). Alder buds also have a higher value than do the catkins.

A seasonal trend is evident in the willow species for which adequate sampling was done (Figure 4) which correlates with the general findings summarized by Golley (1961). It was not practical to separate leaf buds from catkin buds for individual analysis. It appears that caloric values of buds remain relatively constant throughout the fall and winter months, but rise during May when sap rises to the buds prior to catkin flowering, which occurs in late May. After flowering, the values fall to a seasonal low in June. Leaves have a value similar to that of wintering buds.

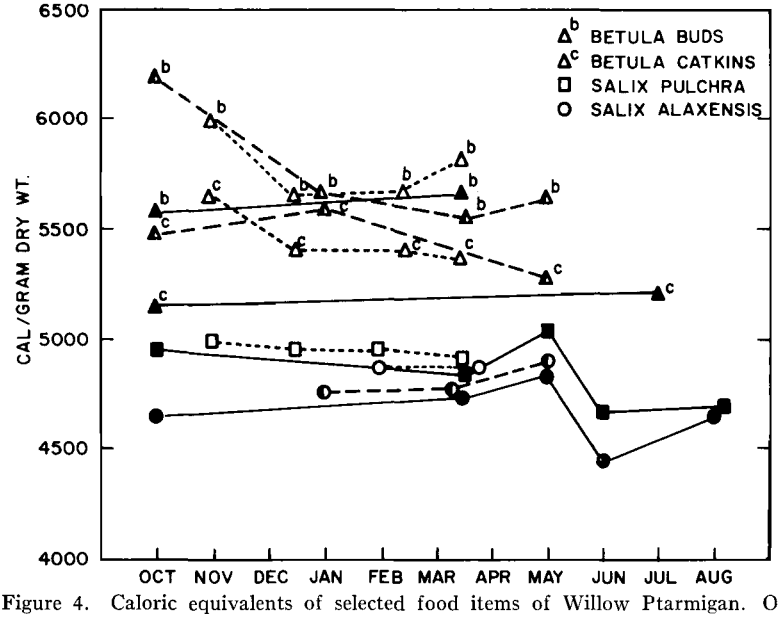

Figure 4. Caloric equivalents of selected food items of Willow Ptarmigan. Open symbols represent samples from Bettles and Crevice Creek; half-closed symbols are from Anaktuvuk; closed symbols are from Umiat.

The average caloric content available per 100 grams of dry food in the average crop has been calculated by multiplying the average per cent occurrence of each item in the crop times its appropriate caloric equivalent for each season (Figure 5). There is a gradual decline in caloric content of the total diet throughout the winter at Bettles and Crevice Creek. At Umiat and Anaktuvuk, the value remains relatively constant in winter, but drops in summer and rises again in the fall. The abrupt decline in summer is due to selection of herbaceous plants, leaves, and berries which have a lower caloric value than the buds used in winter. However, the total variation in caloric content of the average crop at Bettles and Crevice Creek from November to April is only 3.6 per cent, at Anaktuvuk from October through May, 5.7 per cent, and at Umiat where the birds are present throughout the year, 8.7 per cent. This low variation in caloric content of the diet points out a stable relationship between the plants available and those selected by the ptarmigan.

In speaking of caloric equivalents of foods in relation to diet, one obvious problem is the lack of knowledge of how much the individual can extract from the total available calories. This can only be determined through tests to determine amounts of food eaten and excrement produced and by knowing their respective caloric values. Experiments are currently underway to measure these factors.

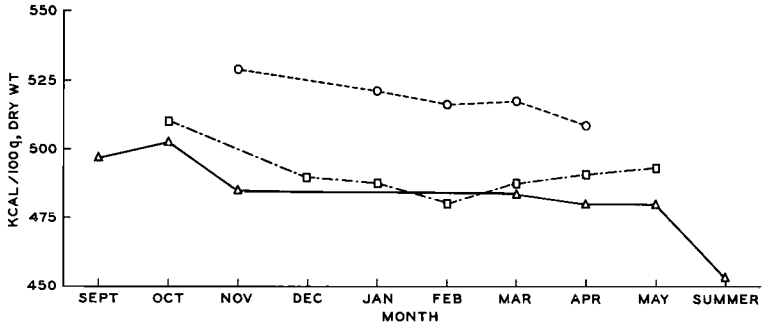

Figure 5. The average caloric content of Willow Ptarmigan crops expressed as kcal/100 g of crop contents by dry weight. Summer represents June, July, and August. Circles are for Bettles and Crevice Creek; squares for Anaktuvuk; and triangles for Umiat.

It is apparent that northern Alaskan Willow Ptarmigan depend more heavily on willow throughout the year than other populations thus far investigated. Seiskari (1957) showed that from January through March, Finnish birds depend on birch and willow almost equally, which together make up 44 to 82 per cent of the diet. Heather (*Calluna vulgaris*) and *Vaccinium* make up the bulk of the remainder. Peters (1958), studying the diet of Willow Ptarmigan in Newfoundland, showed that during the fall, *Vaccinium* spp. berries make up over one half of the diet. During late fall birds shift to buds and twigs of, chiefly, *Vaccinium* spp., birch, and alder. The total lack of willow in the diet is a result of its apparent unavailability in the habitat.

A preliminary survey of diets of Willow Ptarmigan in the Alaska Range in central and southern Alaska by R. B. Weeden and L. N. Ellison (MS) indicated that these birds are dependent on willow, but not to the same extent as the birds in northern Alaska. During winter 79 per cent of the diet of birds of the Alaska Range consists of willow buds and twigs. In the fall birds eat 36 per cent of their diet as willow buds, twigs, and leaves, in the spring, 67 per cent, and in the summer, 28 per cent; the remainder consists mainly of blueberries (*Vaccinium uliginosum*).

Rock Ptarmigan in some areas consume willow to the same extent as northern Alaskan Willow Ptarmigan. Gelting (1937) showed that winter Rock Ptarmigan in Greenland eat from 10 to 77 per cent of their diet as willow (*Salix arctica*). However, many of his monthly samples were small (one or two birds) and an average value for the winter probably is closer to 50 per cent. The remainder of the diet consists mainly of *Dryas octopetala* leaves. During summer, there is a definite selection of *Polygonum*

viviparum bulbils and spikes, but these birds do not depend on berries at any season.

Alaskan Rock Ptarmigan eat birch and *Vaccinium* berries rather than willow since these plants are more abundant in the birds' habitat on the higher hillsides (Weeden and Ellison, MS).

From these and other studies (Holmboe, 1924; Nordhagen, 1928; Wilson and Leslie, 1911) it appears that Willow Ptarmigan make some selection in their diet in that they consume only willow when both willow and alder are present in equal abundance. Robert B. Weeden (pers. comm.) has evidence which suggests that when Rock and Willow ptarmigan are feeding together in areas of mixed willow and birch the Willow Ptarmigan select the willow and the Rock Ptarmigan consume the birch. However, the nutritional requirements of Willow Ptarmigan can be met in the total absence of willow in the habitat, as in Newfoundland.

SUMMARY

Analyses were made of the crop contents of 540 Willow Ptarmigan collected throughout the year at four localities in the Brooks Range of northern Alaska. In winter, the birds depend on the buds and twigs of willow (*Salix* spp.) for their nutrition; up to 94 per cent of the total diet is willow and 80 per cent of that may be of a single species (*S. alaxensis*). After fall migration southward, the population spreads out over 200 miles from the Colville River at the north to the Koyukuk River to the south of the Brooks Range. Variations in amount of snow cover and height of plants restrict the use of certain willow species and dwarf birch (*Betula glandulosa*) in the north during winter, but farther south, willow and birch reach greater heights and remain available throughout the winter. Alder (*Alnus crispa*) is abundant but is seldom used, perhaps because of its chemical composition which may make it unpalatable. As snow melts, the birds depend more on willow leaves, herbaceous plants, and berries.

Caloric values of foods eaten by ptarmigan indicate that birch has a higher caloric content than willow at any season. The caloric content of willow remains relatively constant during winter but rises in spring when catkin buds swell prior to development. In early summer, opened catkins have a low value. Leaves were approximately equivalent in value to winter buds. The caloric content of the average diet remains nearly constant throughout the winter, but drops in summer, because of the use of herbaceous plants and berries whose caloric equivalents are less than that of winter willow buds. Birds wintering in the south of the range consume a diet which is higher in caloric content than that of birds farther north because of the former's use of larger amounts of birch.

From this study and others it is apparent that Willow Ptarmigan are

well adjusted to deriving their nutritional and energy requirements from a number of different diets. The chief dietary component is willow when it is readily available in the locality in which the birds occur, but it is not a necessity for existence of the species.

LITERATURE CITED

BLISS, L. C. 1962. Caloric and lipid content in alpine tundra plants. Ecology, **43**: 653–757.

GELTING, P. 1937. Studies on the food of the East Greenland ptarmigan. Meddelelser om Grønland, **116**(3): 1–96.

GOLLEY, F. B. 1961. Energy values of ecological materials. Ecology, **41**: 581–584.

HOLMBOE, J. 1924. What the Willow Grouse lives on in Norway. Bergen Museum Aarbok 1922 and 1923. Naturvidenshapelig rekke, no. 5.

IRVING, L. 1960. Birds of Anaktuvuk Pass, Kobuk and Old Crow. U. S. Natl. Mus., Bull. 217.

IRVING, L., AND S. PANEAK. 1954. Biological reconnaisance along the Ahlasuruk River east of Howard Pass, Brooks Range, Alaska with notes on the avifauna. J. Washington Acad. Sci., **44**: 201–211.

IRVING, L., G. C. WEST, AND L. J. PEYTON. 1965. Organization of migration of arctic Willow Ptarmigan (*Lagopus lagopus*). Bull. Ecol. Soc. Amer., **46**: 123–124.

IRVING, L., G. C. WEST, AND L. J. PEYTON. 1967*a*. Migration of Willow Ptarmigan in arctic Alaska. Arctic, in press.

IRVING, L., G. C. WEST, AND L. J. PEYTON. 1967*b*. Winter feeding program of Alaskan Willow Ptarmigan shown by crop contents. Condor, **69**, in press.

NORDHAGEN, R. 1928. Willow Grouse and berries. Bergen Museum Aarbok 1928. Naturvidenshapelig rekke, no. 2.

PETERS, S. S. 1958. Food habits of the Newfoundland Willow Ptarmigan. J. Wildl. Mgmt., **22**: 384–394.

SEISKARI, P. 1957. [On the winter feeding of the Willow Ptarmigan.] Suomen Riista, **11**: 43–47.

WILSON, E. A., AND A. S. LESLIE. 1911. Observation on the food of grouse, based on an examination of crop contents. Pp. 67–87 *in* The grouse in health and disease. London, Smith, Elder and Co.

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