FOODS OF ROCK AND WILLOW PTARMIGAN IN CENTRAL ALASKA WITH COMMENTS ON INTERSPECIFIC COMPETITION

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THE value of much of the past work on foods of Alaskan ptarmigan (*Lagopus* spp.) has been severely limited by sporadic collecting and small samples. The work of West and Meng (1966) on Willow Ptarmigan (*L. lagopus*) in arctic Alaska, and of Roberts (1963) on Willow and Rock Ptarmigan (*L. mutus*) in central Alaska are prominent exceptions. The former study was restricted to the central Brooks Range population of Willow Ptarmigan and emphasized winter foods. Roberts' work left seasonal gaps where few collections were available, and his data are not easily compared with West and Meng's or mine because he analyzed samples by volume displacement rather than by oven dry weight.

By combining data from ptarmigan crops collected by the Alaska Department of Fish and Game in Alaska since 1959, I now have enough information to show the kinds of foods Rock Ptarmigan select throughout the year in central Alaska and the species Willow Ptarmigan choose from August to early May. These data establish calendar dates for normal seasonal changes in diet, particularly for Rock Ptarmigan, and allow a comparison of the choices made by *mutus* and *lagopus* in the central part of the state. Winter samples of Willow Ptarmigan from other parts of Alaska and neighboring Yukon allow limited regional comparisons.

MATERIAL AND METHODS

I have included data from 665 Willow and 743 Rock Ptarmigan crops examined during 1959–67. These were from a number of areas and seasons, but mostly from fall and winter collections made south of the Arctic Circle (Figure 1).

Crops were examined when fresh or after preservation in a weak solution of formaldehyde. Contents were sorted, identified, dried at 80°C until no further weight loss could be detected, and immediately weighed to the nearest 5 mg. Crops that contained no single item more than 5 mg in dry weight were discarded.

All items found in each crop were recorded and listed in preliminary tabulations. This report includes only items comprising 1 per cent or more of the total quantity of food in a group of crops from one area and season; people wanting complete listings may write me for them.

Study of items eaten by Rock Ptarmigan suggested that average seasons in central Alaska are defined best as follows: winter, 11 October to 9 May; spring, 10 May to 5 June; early summer, 6 June to 31 July; late summer, 1 August to 31 August; fall, 1 September to 10 October. Data from young Rock Ptarmigan showed that chicks eat somewhat different foods from adults in early summer but not in late summer; the tabulations reflect these findings.

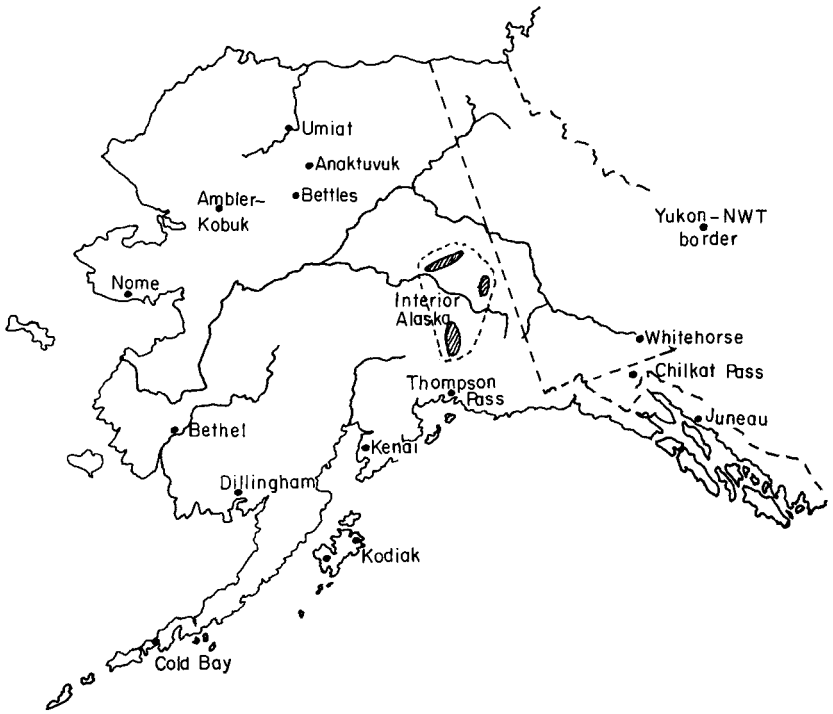

Figure 1. Collection localities (all places labelled).

RESULTS

Rock Ptarmigan.—Seasonal changes in the diet of Rock Ptarmigan from interior Alaska are shown in Table 1.

Catkins and leaf buds of *Betula nana* and *B. glandulosa* (indistinguishable in crops and both called "dwarf birch" here) dominate the Rock Ptarmigan's diet when snow covers the ground to a depth of more than a few inches. Buds of willows (*Salix* spp.) occurred in two-thirds of the crops examined, but were only 6 per cent of the total oven-dry weight. Catkins of *Alnus crispa* (alder), found in far fewer crops than *Salix* or *Betula*, made up 4 per cent of the winter sample. Twenty-nine other items were found in the crops, but only *Vaccinium uliginosum* (bilberry) and *Vaccinium vitis-idaea* (mountain-cranberry) berries comprised 1 per cent or more of the total weight. Twenty-four of the 27 other items were from plants that would be covered completely by 1 foot of snow. These items occurred mainly in crops collected in years when heavy snows did not come until after mid-October, or in crops from birds shot in windblown areas with thin or patchy snow.

TABLE 1
PERCENTAGES OF MAIN FOODS IN CROPS OF 719 ROCK PTARMIGAN FROM INTERIOR ALASKA

Food item	Winter[1] (309 crops)		Spring (41 crops)		Early summer (adults) (28 crops)		Early summer (chicks) (18 crops)		Late summer (75 crops)		Autumn (248 crops)	
	Wt[2]	F[3]	Wt	F	Wt	F	Wt	F	Wt	F	Wt	F
Betula spp. (catkins, buds)	86	97	31	73	6	14	—[4]	11	13	61	51	79
Vaccinium uliginosum (berries)	2	29	11	27	1	4	4	16	9	44	13	60
Empetrum nigrum (berries)	—	20	16	46	2	14	6	22	25	50	10	46
Vaccinium vitis-idaea (berries)	1	15	10	34	8	33	6	27	3	17	2	24
Dryas octopetala (leaves)	—	10	11	56	13	60	2	27	6	36	3	48
Salix spp. (buds, twigs)	6	69	12	44	13	14	0	0	0	0	10	59
Carex spp. (seeds)	—	8	0	0	—	2	9	27	4	32	4	40
Polygonum viviparum (bulbils)	—	3	0	0	14	29	47	56	1	4	2	18
Salix spp. (leaves)	0	0	0	0	15	33	11	27	1	18	1	5
Alnus crispa (catkins)	4	13	—	2	0	0	0	0	0	0	0	0
Alnus crispa (leaves)	0	0	0	0	3	4	0	0	0	0	0	0
Anemone spp. (leaves)	0	0	—	5	2	14	0	0	1	12	—	6
Arctostaphylos alpina (berries)	0	0	—	2	0	0	0	0	1	11	0	0
Betula spp. (leaves)	0	0	0	0	5	11	0	0	0	0	0	0
Dryas octopetala (flowers)	0	0	0	0	3	25	0	0	0	0	0	0
Equisetum spp. (tips)	0	0	3	5	0	0	0	0	0	0	0	0
Lupinus arcticus (leaves)	0	0	1	5	0	0	0	0	0	0	0	0
Moss fruiting bodies	0	0	0	0	—	5	2	22	0	0	0	0
Oxytropis spp. (leaves)	0	0	—	10	9	39	—	6	9	37	—	9
Polygonum bistorta (seeds)	0	0	0	0	0	0	—	6	4	27	—	12
Saxifraga spp. (capsules)	0	0	0	0	0	0	3	27	0	0	0	0
Unidentified leaves	0	0	1	17	3	33	1	83	3	47	—	81
Unidentified flowers	0	0	1	7	—	8	0	0	0	0	0	0
Lepidoptera larvae	0	0	0	0	—	9	4	27	13	23	0	0
Snails (*Succinea* spp.)	0	0	—	2	0	0	4	11	3	3	0	0
Total oven-dry weight (g)	1,731.63		24.53		23.26		14.12		65.62		366.30	
Mean wt. per crop (g)	5.60		0.60		0.83		0.78		0.87		1.48	

[1] Calendar dates of seasons in text.
[2] Weights are oven-dry weights.
[3] F = frequency, or percentage of crops containing item.
[4] Oven-dry weight less than 1 per cent of the total for season.

Dwarf birch seems to be the most important winter food of Rock Ptarmigan throughout the State. At Anaktuvuk Pass 10 birds shot between 20 March and 7 May had crops containing 93 per cent *Betula*, 4 per cent *Alnus*, and almost 3 per cent *Salix*. Nine crops from Rock Ptarmigan shot in April near Kobuk and Ambler contained 92 per cent *Betula*, almost 7 per cent *Alnus*, and a small amount of *Salix*. *Betula* comprised 99.7 per cent of the crop contents of five Rock Ptarmigan shot in late April and early May near Dillingham southwestern Alaska. Five full crops of Rock Ptarmigan shot near Juneau late in February 1953 and examined by Harvey Roberts, Alaska Cooperative Wildlife Research Unit, contained nothing but *Betula* buds and catkins.

Lauck's Testing Laboratory, Seattle, analyzed nutritional content of samples of *Betula* buds and catkins from Rock Ptarmigan crops collected in seven localities in central and northern Alaska in September, December, February, March, and April. The samples (based on dry weights) contained 12.4 to 14.2 per cent protein, 7.8 to 14.3 per cent fat, and 39.9 to 57.1 per cent nitrogen-free extract. Caloric values ranged from 5,650 to 5,970 calories per gram of dry weight, exactly the same range as samples of *Betula* in northern Alaska reported by West and Meng (1966). These caloric values are roughly 17 per cent higher than those of *Salix* winter buds, and about the same as those of *Alnus crispa* buds and catkins, as reported by those authors.

The mean weight of Rock Ptarmigan crop contents (Table 1) changes drastically during the year. Winter crops contain a lot of food because collections coincide with feeding periods (ptarmigan and biologists both seek shelter at night) and because ptarmigan are forced to feed fewer times in 24 hours and to eat more each feeding period. Mean weight of crop contents drops sharply in spring with lengthening daylight, and stays low until autumn. West and Meng (1966) present similar findings for Willow Ptarmigan in northern Alaska.

Spring is characterized by the melting of snow and initial growth of vegetation. Most Rock Ptarmigan continue to eat *Betula* buds and catkins in spring, but in sharply reduced amounts and proportions. Fewer birds eat *Salix* buds than in winter, but the amount taken per feeding stays about the same; thus the percentage of *Salix* doubled to 12 per cent of the total dry weight. Bilberries, mountain-cranberries, and crowberries (*Empetrum nigrum*) remain on the plants until spring and are eaten in quantity by ptarmigan when the snow melts. *Dryas octopetala* (mountain avens, or dryas) leaves were the only leaves to appear in significant quantity in spring crops, although many alpine plants flower or leaf out by late May and early June in central Alaska (Weeden, 1968).

June and July are the months when flowers and leaves are produced in greatest quantities in central Alaska. Snow is almost completely gone from ptarmigan habitat. Seeds and fruits are not yet abundant or not mature. At this period, which I have designated as early summer, adult Rock Ptarmigan eat fewer *Betula* buds and catkins than at any other time of year. Oddly, *Salix* buds and twigs continue in adult Rock Ptarmigan crops in the same relative amounts as in spring. Berries are much less important, as last year's crop is almost gone, except for mountain-cranberries which persist on vines until late summer, and new fruits are unripe. Leaves of *Salix, Dryas octopetala*, and *Oxytropis* spp. made up 37 per cent of oven-dry weights of the crops sampled, and leaves of other species together amounted to another 13 per cent by weight. *Polygonum viviparum* bulbils were a significant new item in the samples. The number of different food items taken by Rock Ptarmigan probably is greater in early summer than at any other season.

Only 18 crops of Rock Ptarmigan chicks with more than trace amounts of food were available for study. These contained fewer leaves than crops of adults from the same area and season (14 per cent as opposed to 50 per cent); slightly more berries (16 vs. 11 per cent), most of them unripe; and far more bulbils of *Polygonum viviparum*. Snails and larvae of various Lepidoptera made up 8 per cent of the dry weight of the 18 chick crops examined.

In August Rock Ptarmigan eat fewer leaves and more berries. Interestingly, over half the crops in the August sample contained *Betula* buds and catkins, amounting to 13 per cent of the total dry weight. As very little snow falls in August (in most years there is none), it appears that the birds sample *Betula* extensively long before snow makes alternate foods unavailable.

The appearance of Lepidoptera larvae in the August crops merits comment. Nearly all the caterpillars were in the crops of 20 birds shot 25 and 27 August 1952 at Eagle and Twelve-mile Summits, Steese Highway, by the Alaska Cooperative Wildlife Research Unit. Roberts (1963), reporting on a different collection from the same area, season, and year, found these larvae (Phalaenidae) in 5 of 16 crops, totaling 9.4 per cent of combined crop volume. None of the 55 other crops in late summer samples from 1959 to 1967 contained caterpillars. The birds must have taken advantage of an unusual abundance of caterpillars in 1952—the best example of opportunism I have found in this examination of ptarmigan food habits.

Plants achieve winter condition rapidly in September in central Alaska. The essential difference between fall and winter, as far as ptarmigan are

TABLE 2
MAIN WINTER[1] FOODS OF WILLOW PTARMIGAN IN ALASKA AND YUKON

Area (no. specimens)	*Salix* spp.	*Betula* spp.	*Populus* spp.	*Empetrum nigrum*	Misc. items
Umiat[2] (161)	89[3]	4	—	—	7
Anaktuvuk Pass[2] (252)	91	5	—	—	4
Crevice Creek[2] (65)	79	19	—	—	2
Bettles[2] (52)	62	27	11	—	—
Nome (43)	96	2	—	—	2
Bethel (78)	77	16	1	1	5
Kodiak (54)	89	—	—	7	4
Kenai (13)	78	2	20	—	—
Thompson Pass (9)	100	—	—	—	—
Interior (337)	89	10	1	—	—
Chilkat Pass, B.C. (15)	98	—	—	—	2
Whitehorse (12)	100	—	—	—	—
Yukon-NWT Border (6)	85	15	—	—	—

[1] 10 October to 9 May, except that West and Meng's (1966) data for northern Alaska include all of October–May.
[2] Approximated from West and Meng (1966).
[3] Figures are per cent by oven-dry weight.

concerned, is the fact that all seeds, fruits, and buds produced in the alpine habitats are available in fall before snow is deep. The arbitrary date of 10 October, chosen to delineate the end of autumn and beginning of winter, is simply an average date at which persistent snow is deep enough to cover all but woody vegetation. As might be expected, the fall diet of Rock Ptarmigan is characterized by a sharp increase in consumption of dwarf birch catkins and buds, continued use of berries (one-fourth of total dry weight in my specimens), and much-diminished utilization of leaves. Hard frosts usually kill deciduous leaves in mid-September, and certainly influence the seasonal change in diet of ptarmigan.

Willow Ptarmigan.—West and Meng (1966) found *Salix* buds and twigs to be the most important food of Willow Ptarmigan in northern Alaska in winter. I found the same to be true in central Alaska and in other scattered locations in Alaska and Yukon (Table 2). Poplar (*Populus tremuloides*, *P. balsamifera*) buds were eaten in quantity during 2 winter months in Bettles, and Willow Ptarmigan collected near Kenai in January also had eaten some *Populus* buds. *Empetrum* berries occurred in crops of Willow Ptarmigan shot in Bethel and Kodiak, indicating occasional thin snow cover in these areas during winter.

Sixteen crops from Willow Ptarmigan shot from 15 November to 4 February near Cold Bay, at the tip of Alaska Peninsula, contained 45 per cent *Salix* buds, 27 per cent *Rubus spectabilis* (salmonberry) buds, and 26 per cent *Empetrum nigrum* leaves. In a letter dated 25 March 1964 Robert Jones, Refuge Manager, Aleutian Islands National Wild-

TABLE 3

PERCENTAGES OF MAIN LATE SUMMER AND FALL FOODS OF 72 WILLOW PTARMIGAN FROM INTERIOR AND WESTERN ALASKA

Food item	Late[1] summer (18 crops)		Autumn (Interior) (27 crops)		Autumn (Nome) (27 crops)	
	Wt	F[2]	Wt	F	Wt	F
Salix spp. (buds,twigs)	3	22	55	78	83	96
Betula spp. (catkins, buds, twigs)	2	22	2	18	3	37
Salix spp. (leaves)	36	61	6	44	—[3]	4
Vaccinium uliginosum (berries)	20	66	15	52	—	7
Vaccinium vitis-idaea (berries)	7	22	2	7	0	0
Empetrum nigrum (berries)	—	17	3	30	11	74
Equisetum spp. (tips)	6	50	13	22	—	11
Vaccinium uliginosum (leaves)	8	33	2	30	—	4
Carex spp. (seeds)	5	17	—	17	—	4
Polygonum viviparum (bulbils)	9	22	0	0	0	0
Saxifraga spp. (capsules)	1	11	0	0	0	0
Unidentified flower	—	6	2	15	0	0
Unidentified leaves	1	11	—	7	—	15
Unidentified insects	0	0	0	0	2	33

[1] For seasons, see text.

[2] F = frequency, or percentage of crops containing item.

[3] Indicates items with less than 1 per cent of the group total. All figures refer to percentages by oven-dry weight.

life Range, said that he could not remember a single instance in 15 years when snow cover was complete in the Cold Bay area. In this relatively mild climate, with no snow to interfere with free choice of foods, Willow Ptarmigan still feed on buds of woody plants to a considerable degree.

I do not know when Willow Ptarmigan change from winter to spring diets. West and Meng (1966) did not present their data in such a way that this information is available, but the ptarmigan they collected 1 to 10 May in Anaktuvuk Pass had begun to eat peristent green leaves of *Dryas* spp., indicating the start of thawing conditions. Roberts (1963) had few spring collections of *L. lagopus*. However, it is likely that the change occurs at the same time as among Rock Ptarmigan, or in mid- to late May in interior Alaska.

Data on early summer foods of Alaskan Willow Ptarmigan also are scarce. West and Meng (1966) pooled their data for June, July, and August. Roberts (1963) looked at only six crops from June and July. My own early summer collections are too small to be useful.

Table 3 lists foods in crops of Willow Ptarmigan collected in late summer and fall in interior Alaska and near Nome. August crops contained 45 per cent leaves, 27 per cent berries, and 15 per cent seeds or bulbils. Fall crops from the interior showed a rapid upsurge in consumption of buds and twigs of willow, and a rapid drop in utilization of willow leaves.

Near Nome Willow Ptarmigan shot late in September were eating mainly willow buds and crowberries.

Ten crops from Willow Ptarmigan shot in southern Kodiak Island 11 November 1951 (donated by the Department of Wildlife Management, University of Alaska) contained 67 per cent willow twigs and buds, 25 per cent *Arctostaphylos uva-ursi* berries, and small amounts of *Andromeda polifolia* leaves, *Betula* twigs and buds, crowberry leaves, and mountain-cranberries. Although this collection falls within the "winter" period, the birds obviously were able to feed on snow-free areas. (All of the species in the crops, except *Betula*, have evergreen leaves.) The composition of the diet of these birds is comparable to that of September and early October specimens from central Alaska.

DISCUSSION

In most of Alaska all ptarmigan (including *L. leucurus*; see Weeden, 1967) rely almost entirely on buds, twigs, and catkins of deciduous shrubs for food during the 5 to 7 months when snow covers nonwoody plants. Evidence from coastal areas with little or no snow, where buds and twigs of shrubs are taken in large quantity even though other sorts of food are available, suggests that these catkins, buds, and twigs may be among the most nutritious plant foods available to ptarmigan in the North. The tendency for ptarmigan to begin eating winter buds of various shrubs up to 2 months before snow falls in central Alaska also supports this idea.

In mid-summer, despite a very wide potential choice of plant foods, Rock and Willow Ptarmigan rely on a relatively small number of species for most of their food, although their choices are more varied than in winter. The data available from this study indicate that animal foods are unimportant to adult ptarmigan in summer, except when forms like snails, grasshoppers, or caterpillars are unusually abundant.

Two transitional periods separate the long winter and short summer dietary periods. The spring transition occurs during the height of territoriality and egg-laying in interior Alaska; the environment is characterized by disappearing snow and beginning plant growth. The fall transition spans a longer period (almost 2 months) when ptarmigan are developing their winter plumage, forming flocks, displaying, and rearranging their social structure in preparation for early winter migrations (Weeden, 1964). For the most part there are no food items taken solely in spring or fall. Rather, the diet consists of winter and summer items that are waxing or waning in quantity, as appropriate to the season.

Anyone interested in population control mechanisms in Galliformes will be impressed with the possibilities for critical nutritional shortages implied in the dietary information presented for ptarmigan. As Gullion

(1966) points out, whenever a bird relies on one kind of food for a long period each year, there is the chance that quantitative and qualitative shortages could seriously increase mortality or reduce reproductive success. The three aspects of this question that should be studied concurrently are a) yearly changes in winter food quality or quantity on a given piece of ptarmigan habitat, b) studies on captive ptarmigan to find out critical levels of intake, using the normal winter foods, and c) actual changes in populations of ptarmigan.

Another potentially important time of year is spring, when energy demands increase because of reproductive and molt activities. Ptarmigan are normally not in poor body condition in spring, at least not in comparison to their leanness in early or mid-summer. Nevertheless it is entirely possible that something extra is needed nutritionally in spring, to allow maximum production of high-quality eggs. Detailed studies are needed to discover whether rising nutritional quality of winter foods (when sap rises to buds before flowering; see West and Meng, 1966) or timely growth of new leaves or alpine flowers, are critical for successful reproduction of ptarmigan.

Because North American Willow, Rock, and White-tailed Ptarmigan select different breeding habitats, they do not compete with each other for food in the period May through September. Their choice of summer foods probably is based on selection of nutritious and commonly available items, which differ geographically according to the range of plant species present. The shrubby interface between wood and tundra is the habitat where all species of ptarmigan live in winter in central Alaska. As I mentioned in an earlier paper (Weeden, 1967) competition in this habitat may have had noticeable effects on food selection by each species.

The tendency for each kind of ptarmigan to select one food source in winter probably has been accompanied by morphological and behavioral specializations. An obvious one is the difference in bill shape in various ptarmigan, with Rock Ptarmigan having narrow bills, Willow Ptarmigan having broad, deep bills, and White-tailed Ptarmigan having bills of intermediate size and shape. Catkins and buds of dwarf birch are very small (2–5 mm), whereas willow buds the Willow Ptarmigan commonly eat are larger (5–15 mm), and that species often takes twigs 15–20 mm in length. The bill of *L. mutus* may be more efficient for picking up small items; this is indicated also by analysis of 375 *mutus* and 318 *lagopus* gizzards, which showed that 92 per cent of the grit particles in Rock Ptarmigan gizzards were 2 mm wide or smaller, whereas 64 per cent of the grit Willow Ptarmigan ingested was larger than 2 mm. Alaskan White-tailed Ptarmigan eat large amounts of the big aments of *Alnus* spp., but

also eat significant quantities of dwarf birch and willow buds; this ties in with their larger bill size, relative to Rock Ptarmigan.

Behavioral specializations may include such things as the relative frequency with which *L. lagopus* perches in tall shrubs while feeding and the tendency for *L. mutus* to scratch through snow to get at foods on the ground. Quantitative study of these characteristics is needed to see how important they are in preventing overlap in winter food choices of ptarmigan in areas of sympatry.

If interspecific competition narrows food selection in winter, lack of competition should allow wider food choice, if the possibility for such a choice is present. This could be tested by comparing winter foods of Rock Ptarmigan (for example) in regions where the species is the only member of the genus present, with those in regions where it is in contact with one or two other species. Unfortunately the only thorough studies of winter foods of *L. mutus* known to me are those of Gelting (1937) in Greenland, where only *mutus* lives, and Watson (1964) in Scotland, where *mutus* and *lagopus* breed. Studies of winter foods of *mutus* in Iceland, Japan, and the European Alps would be especially interesting, as would comparative studies of *mutus* and *lagopus* in Siberia and Scandinavia. Previous work in those latter areas is hard to interpret because of lack of information on whether collections were from areas where the two ptarmigan were actually in contact with each other in winter. Present studies in Iceland (Finnur Gudmundsson, letter dated 9 April 1968) will provide excellent data for region-to-region comparisons as suggested here.

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SUMMARY

A collection of 743 Rock Ptarmigan crops from all seasons of the year and 663 Willow Ptarmigan crops from August through April was analyzed for oven-dry weight of food items.

Throughout Alaska, Rock Ptarmigan eat mainly buds and catkins of dwarf birch in winter (11 October to 9 May). In spring (10 May to 5

June) the transition to the varied early summer (6 June to 31 July) diet of leaves and flowers is fairly quick. The late summer (1–31 August) diet is characterized by decreased consumption of leaves and flowers and increased consumption of berries and seeds. Animal matter is taken opportunistically, but rarely in large amounts. The fall period is essentially a long transition from the seeds and fruits of August to the monotonous diet of buds and catkins of winter.

The pattern among Willow Ptarmigan seems similar to that of Rock Ptarmigan from August to early spring in central Alaska. In coastal areas where there is little snow, Willow Ptarmigan eat a wider variety of foods in winter, but still feed heavily on buds and twigs of deciduous shrubs. Throughout Alaska the main winter food of Willow Ptarmigan is *Salix* spp. buds and twigs.

Given the demonstrated heavy dependence of the Rock and Willow Ptarmigan on a very few types of winter food, quantitative or qualitative shortages in winter foods could have serious direct and indirect population effects. The short period of dietary transition in spring could be critical also, as heavy energy demands for molting and breeding occur at that time.

Interspecific competition may have a bearing on winter foods selected by Rock, Willow, and White-tailed Ptarmigans in areas of sympatry. Bill shape seems to be an adaptive feature correlated with the winter food specializations observed, and behavioral specializations such as perching or scratching for food may be important too.

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