SEASONAL AND GEOGRAPHIC VARIATION IN THE FOODS OF ADULT WHITE-TAILED PTARMIGAN

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As I studied various aspects of the life, distribution, and population fluctuations of ptarmigan (*Lagopus mutus*, *L. lagopus*, *L. leucurus*) over the past 10 years, I realized the importance of obtaining quantitative data on the food habits of these birds. The fund of information on the foods of White-tailed Ptarmigan (*L. leucurus*) in the literature is amazingly low, there being only reports of scattered and fragmentary collections. For that reason I began to collect crops of this species, and have summarized the results of crop examinations in this paper.

METHODS

Crops were available from White-tailed Ptarmigan collected in 23 localities from Colorado to Alaska (fig. 1). These localities have been placed in four groups: Colorado–Wyoming, Coastal British Columbia–Washington, Central British Columbia– Alberta, and Alaska–Northern British Columbia. The food data are presented by region in tables in which crops collected in roughly the same area and at comparable times of year are combined in one column. For example, if two collections were made in a single locality, one in November and another in March, I combined the information in the belief that the same general feeding conditions prevailed throughout that time. Data from crops collected at different times during the period of spring thaw or autumn snow accumulation, on the other hand, could not be pooled safely. In a few cases crops from one locality and season had to be treated separately because of differences in techniques of measurement.

Three methods were used at different times to analyze the contents of crops. In 1957 I measured the volume of items in fresh crops by water displacement in cylinders graduated to 0.1 cm³. The crops from the U.S. Fish and Wildlife Service collection were too dry to treat that way; so food items were weighed, air-dry, to the nearest 0.001 g. Alaskan material collected from 1959 through 1965 was measured volumetrically by water displacement, the volume being estimated to the nearest 0.5 cm³. Food items then were dried at 80° C until weights remained constant (from one to three days, depending on type of food), and weighed to the nearest 0.005 g. Young-of-the-year collected after 31 August were included in this summary.

Items making up less than 5 per cent of the combined volume or weight of crop contents from one season and locality have not been included in the tables. For that reason many species of plants found in the crops, and all animal food items, have been omitted. Persons interested in a complete list of foods may write to the author.

Plant parts are abbreviated in the tables as follows: B (buds), T (twigs), L (leaves), FR (fruit), C (catkins), and FL (flowers). Per cent frequency in the tables refers to the proportion of sampled crops containing the food item identified.

RESULTS AND DISCUSSION

The results of the crop analysis are presented in tables 1 through 5. Two additional crops from Wyoming were examined. They were collected on 5 July 1911 in the Medicine Bow Mountains. Both crops contained *Carex* seeds (72 per cent of combined crop contents by weight). *Dryas* leaves, *Salix* leaves, and *Draba* (?) flowers were found in one crop each, and each made up 5 per cent of the total weight of the



Figure 1. Locations of White-tailed Ptarmigan collections used in this study.

combined contents of both crops. Insects (*Coleoptera*) were 5 per cent of the pooled weight but were present in only one crop.

Salix leaves, Dryas leaves, and Dryas flowers were the most important foods in my sample of nine White-tailed Ptarmigan collected shortly after the spring thaw began. Empetrum berries from the previous year's growth were important in two crops collected early in June in the Hazelton area of central British Columbia. Apparently Salix leaves also are eaten frequently in summer, along with Ranunculus leaves, Polygonum fruits, and seeds of grasses and sedges. The sample of spring and summer crops available to me is very small, however, and many more collections are needed in all areas. One interesting point not clarified by my data is whether new vegetative growth, more nutritious than the dormant plant materials taken all winter, is available to female White-tailed Ptarmigan before egg-laying begins in spring.

Gallinaceous birds of temperate and arctic-alpine regions typically undergo a radical shift in food habits between late summer and early winter. White-tailed Ptarmigan in Colorado seem to make the change in September and early October (table 1). Early in September the important items in crops of White-tailed Ptarmigan were green leaves (*Salix* spp.) and fruits of low-growing plants (*Draba, Polygonum*) that could be obtained as long as the ground was free of snow. Later in the month *Salix* buds and twigs replaced *Salix* leaves in the diet, and by mid-October the only

TABLE	1
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COMMON FOODS IN CROPS OF 73 WHITE-TAILED PTARMIGAN FROM COLORADO

	Dates of collections												
Food	30/5 % Freq.	%	14/7/03 ^b % % Freq. Wt.		11/9/65° % % Freq. Wt.		3/9/03d 26/9/04e % % Freq. Wt.		17/10/04 ^r % % Freq. Wt.		3/3,	11/03 ^s 3/04 ^h 11/03 ¹ %	
Salix B, T	100	69	_	_	_		85	62	100	60	100	98	
Salix L	_	_	100	34	58	38	_		_	_			
Salix C	_	_	75	6	_	_	_	_			_	—	
Dryas octopetala L	67	9		_	—	_	_	_	84	38			
Dryas octopetala FL		_	75	50	_	_	_	_		—			
Vaccinium L	—	—	25	6	_	—		—	—	_	_		
Polygonum viviparum FR	_	—		—	63	9	_	—	_			—	
P. bistortoides FR	_	—	—	—	_	—	15	8		—		—	
Draba FR	—	—	—	—	58	26	46	8	_	—	_	_	
Saxifraga FR	_			_	37	8		_	_	_	_	_	
Carex FR	_	—	_	-	_	—	54	5	_	—	_	_	
Kalmia polifolia L	17	11	_	_	_	_		_				_	

Bullion Peak, 6 crops.
Hall Valley, 4 crops.
Independence Pass, 19 crops.
Arapaho Peak, 2 crops.
Bullion Peak, 11 crops.
Bullion Peak, 8 crops.
Bullion Peak, 8 crops.

^h Webster, 2 crops.
 ⁱ Bullion Peak, 2 crops.

common item other than Salix buds and twigs was Dryas, a ground-level plant available on windswept ridges. One interesting aspect of the fall diet of Colorado Whitetailed Ptarmigan is the absence of berries in the crops. This is probably due to a scarcity of berry-bearing shrubs in Colorado's alpine habitats (for example, see Marr, Ecosystems of the east slope of the Front Range in Colorado, Univ. Colorado Studies, Ser. in Biol. no. 8, 75-95, 1961).

Salix buds and twigs were dominant in crops collected in September in Washington (table 3), northwestern British Columbia (table 4), and two localities in Alaska (table 5). Berries of *Empetrum* and *Vaccinium* and leaves of *Sedum* made up most of the crop contents of six ptarmigan collected on Vancouver Island (table 2) in September. *Empetrum* berries also were taken by ptarmigan collected in September at Thompson Pass and Summit Lake, Alaska,

White-tailed Ptarmigan become browsers when snow covers all except trees and taller shrubby plants in alpine and subalpine habitats. Like other members of the genus Lagopus, White-tailed Ptarmigan rarely eat conifer needles or buds. Instead they eat buds and twigs of Alnus, Salix, and Betula, the proportion taken of each genus varying with locality. Both my sample of crops from Colorado White-tailed Ptarmigan and Quick's (Condor, 49:233-235, 1951) sample of droppings of ptarmigan in Colorado show Salix to be by far the most important source of winter food in that state. Quick found up to 13 per cent Abies needles in some of his samples. Neither of us recorded Alnus or Betula from crops or droppings. In contrast, Alnus catkins formed 48 per cent of the contents of 43 crops from White-tailed Ptarmigan

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		Dates of collections											
	11/6	/41ª	?/7/	/42 ^b	29/9	/57e							
Food	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt							
Salix L, C	100	92	_	_									
Carex, Poa FR	50	7	100	47	_	_							
Cassiope FL	_	—	100	43	_								
Arctostaphylos alpina FR	_	_	100	9	_	_							
Empetrum nigrum FR		_	_		100	61							
Sedum oregonum L					67	16							
Vaccinium (blueberry) FR	_	_		_	83	12							
Unidentified veg.					83	6							

TABLE 2 COMMON FOODS IN NINE CROPS OF WHITE-TAILED PTARMIGAN FROM COASTAL PREFERENCE COLUMNER AND WARTENGTON

^a Mount St. Helens, Washington, 2 crops. ^b Mount Edward Albert, Vancouver Island, 1 crop. ^c Mount Arrowsmith, Vancouver Island, 6 crops.

collected in Alaska in winter; Salix and Betula comprised 25 and 26 per cent, respectively (table 5, data from columns 4-7 pooled).

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According to Marr (op. cit.), Alnus is sparsely distributed in subalpine habitats of the Front Range, and Quick (op. cit.) said that Alnus and Betula glandulosa were present in small amounts in ptarmigan habitats that he visited. This would account for the scarcity of those foods in the winter diet of Colorado ptarmigan. It

TABLE 3
COMMON FOODS IN NINE CROPS OF WHITE-TAILED PTARMIGAN FROM COASTAL
CENTRAL BRITISH COLUMBIA, AND ALBERTA

	Dates of collections													
-		7/11/19º												
	27/5	/58ª	5/6,	/58 ^b	4/8/	/58ª	28/7	/58°	21/8	/20f	5/9/20			
	%	%	%	%	%	%	%	%	%	%	%	%		
Food	Freq.	Wt.	Freq.	Wt.	Freq.	Wt.	Freq.	Wt.	Freq.	Wt.	Freq.	Wt.		
Salix L	50	25		—	100	79	—					_		
Salix B, T	_		100	73	_	—	—		—	—	86	81		
Carex FR			_			—		—	_	—	29	10		
Cassiope (?) FR		—	_		<u> </u>	—	—			—	29	7		
Dryas octopetala L	100	41				—	—	_	_			—		
Dryas octopetala FL	100	23		—	_		_				—	—		
Empelrum nigrum FR	_	-	50	21	—		—	—						
Poaceae FR	_			_	_		_	—	100	37				
Polygonum viviparum FR					67	13	—	_	_	—	_			
Ranunculus L	_	—		_	—		100	94	100	54				
Unidentified L		_		<u> </u>	—	_			100	9	_			

Baníf Natl. Park, Alberta, 2 crops.
Hazelton, B.C., 2 crops.
Stikine River, B.C., 1 crop.
dorna Lake, B.C., 2 crops.
Waterton Lakes, Alberta, 1 crop.
Baron, Wash., 1 crop.
Bald Mountain, Wash., 7 crops.

TABLE 4

COMMON FOODS IN CROPS OF 18 WHITE-TAILED PTARMIGAN FROM NORTHERN BRITISH COLUMBIA

	Dates of collections													
		5/6/60°												
				30/6,	/581	27/8	/575							
	2/5,	/57ª	18/5	/57Ъ	11/6	/58ª	29/6	/57e	1/7/	/58	7/9/57h			
	%	%	%	%	%	%	%	%	%	%	%	%		
Food	Freq.	Vol.	Freq.	Vol.	Freq.	Wt.	Freq.	Vol.	Freq.	Vol.	Freq.	Vol.		
Salix B, T	100	15	100	81	—		_	_	_	_	43	61		
Salix L		_	100	19	75	80	100	100	67	29	86	14		
Betula glandulosa C	100	83				_		_				_		
Dryas octopetala L		_	_	_	50	7					_			
Dryas otopetala FL			_		25	8		_	_	_		_		
Polygonum viviparum FR			—	_					33	53	_			
Zygadenus elegans FR	—	_		_		_	_	_	33	15		_		
Saxifraga L	—	<u></u>	_		_	—				_	43	12		
Carex FR		_	_								26	7		

Chilkat Pass, 2 crops.
Chilkat Pass, 1 crop.
Chilkat Pass, 3 crops.
d Atlin, 1 crop.
Chilkat Pass, 1 crop.
Chilkat Pass, 3 crops.
g Atlin, 3 crops.
h Chilkat Pass, 4 crops.

is not so easy to understand why *Alnus* is the dominant winter food of Alaskan Whitetailed Ptarmigan, because both *Betula glandulosa* and many species of *Salix* are abundant in places used by White-tailed Ptarmigan in winter (especially in the Alaska Range). I suggest that two factors are involved: the increasing abundance of subalpine *Alnus* as one progresses northwestward from Colorado to Alaska, and increased contact among White-tailed Ptarmigan, Rock Ptarmigan (*L. mutus*), and Willow Ptarmigan (*L. lagopus*) in British Columbia and Alaska.

The species *L. leucurus* probably originated in the southern Rocky Mountains early in the Pleistocene, and very likely has had a complicated history of northward range extensions during interglacial periods, followed by isolation and extinction of northern populations during important glacial advances. During periods of northward movement, some populations of White-tailed Ptarmigan may have lived in areas where *Alnus* was almost the only food available in winter. Areas like this exist today in coastal Alaska (see Heusser, Late Pleistocene environments of North Pacific North America, Amer. Geog. Soc., New York, p. 46, 1960; and Cooper, Ecol. Monographs, 12:1–22, 1942). Birds able to eat *Alnus* presumably would have had an advantage over others, and the ability to utilize this food may have become genetically fixed in northern populations.

In many parts of south-central Alaska, Salix, Betula, and Alnus are common in places used by wintering White-tailed Ptarmigan. In fact, there is more than enough Salix to support the White-tailed Ptarmigan population if it were the only species of ptarmigan present. However, either or both of the other two species of Lagopus winter in the same places as L. leucurus. In those situations the Rock Ptarmigan feeds heavily on Betula, lightly on Salix, and rarely on Alnus; Willow Ptarmigan feed heavily on Salix, lightly on Betula, and rarely on Alnus; and White-tailed Ptarmigan eat all three genera of shrubs but feed most heavily on Alnus (data on L. lagopus

TABLE	5
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COMMON FOODS IN CROPS OF 50 WHITE-TAILED PTARMIGAN FROM ALASKA

	Dates of collections													
		3/23ª /36b	6/9/	/36e	14/9	/64a	24/1		20/10 t Vari yea	ous	4	/658	2/12 to Vari yea	ious
Food	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt.	% Freq.	% Wt.
Salix L	_		100	43	100	98		_						_
Salix B, T	—	—	50	9	_	<u> </u>	100	46	100	57	_	—	58	6
Salix B, T, L	100	71				—	100	53	_			_		
Alnus C	—	_	_			_	—	—	50	39	100	77	94	46
Betula glandulosa B, G	2 —	_		<u> </u>		_			_		100	20	88	46
Dryas L	75	10	_			_		—	_		_			_
Empetrum nigrum FR	25	8	100	46		_			_	_		_		_

^a Mt. McKinley National Park, 3 crops.
^b Summit Lake (Rainbow Mtn.), 1 crop.
^c Thompson Pass, 2 crops.
^d Thompson Pass, 1 crop.
^e Thompson Pass, 9 crops.
^f Little Susitna River, 12 crops.
^g Rabbit Creek, 3 crops.
^g Rabbit Creek, 3 crops.

h Rainbow Mtn., 19 crops.

and L. mutus on file at the Alaska Department of Fish and Game, Fairbanks). Competition among the three ptarmigan may have contributed to the divergence in winter foods noted in areas where all Lagopus live. This intriguing situation deserves much closer study.

SUMMARY

Crops of 167 White-tailed Ptarmigan collected in 23 localities from Colorado to Alaska were examined during this study.

The leaves of Salix and Ranunculus, Dryas flowers, grass and sedge seeds, and *Polygonum* fruits were common items in the scattered spring and summer collections available.

White-tailed Ptarmigan in Colorado ate Salix leaves, Draba fruits, and Polygonum fruits early in September, shifting to Salix buds and twigs and Dryas leaves later in September and October. No berries were found in autumn crops of White-tailed Ptarmigan from Colorado, although fruits of *Empetrum nigrum* and *Vaccinium* spp. were eaten by this bird in the fall in various parts of Alaska and British Columbia.

Colorado ptarmigan apparently subsist mostly on Salix buds and twigs in winter. No Alnus or Betula was found in crops of white-tails from this state. In contrast, Alnus catkins make up an important part of the winter diet of Alaskan white-tails, with Salix and Betula of lesser importance. The difference in winter diet between white-tails from Colorado and Alaska may be due to an increased proportion of Alnus in northern winter ranges, and to competition for fairly restricted food supplies among the three species of Lagopus in Alaska.

ACKNOWLEDGMENTS

Crops were collected and analyzed under a grant from the Arctic Institute of North America in 1957 and 1958, and in the course of work for the Alaska Depart-

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ment of Fish and Game under Federal Aid in Wildlife Restoration Projects W-6-R and W-13-R from 1959 through 1966. Seventy-eight crops were obtained from the collection of the U.S. Fish and Wildlife Service, greatly extending the geographic coverage of the present report. Other crops were donated by Donald R. Flook, Canadian Wildlife Service; Sandra Kogl, College, Alaska; Glenn Rogers, Colorado Department of Game, Fish, and Parks; Leonard Peyton, Laboratory of Zoophysiology, University of Alaska; and Jack Didrickson and Laurence Ellison, Alaska Department of Fish and Game. I am indebted to these people and agencies for their assistance.

My wife, Judith S. Weeden, sorted, weighed, and identified material in crops from the U.S. Fish and Wildlife Service. I appreciate the tediousness of her task, a job made especially difficult because many of the crops had been stored for 50 years. Laurence Ellison and Sandra Kogl helped to analyze most of the specimens obtained in Alaska from 1959 to 1965. Judith Weeden, Laurence Ellison, and George C. West (Laboratory of Zoophysiology, University of Alaska) deserve thanks for the improvements they made in the manuscript.

Department of Fish and Game. State of Alaska, Fairbanks, Alaska, 14 April 1966.