WINTER DIETS, GUT LENGTHS, AND INTERSPECIFIC COMPETITION IN ALASKAN PTARMIGAN

ROBERT MOSS

CLOSELY related species that live in the same region frequently eat different diets, which is usually attributed to interspecific competition for food. Morphological specializations may occur as a result of such competition, and allow each species to utilize its own particular food most effectively. An example of this is the three species of ptarmigan in interior Alaska: Willow Ptarmigan (*Lagopus lagopus*), Rock Ptarmigan (*L. mutus*), and White-tailed Ptarmigan (*L. leucurus*).

In winter the ground is usually covered by snow and all three species browse on shrubs. They often occur in the same place and sometimes in mixed flocks, though more often in flocks of one species. Flocks of each species often use the same pieces of ground at different times, but all three species do not occur on all the available ground. Willow Ptarmigan eat almost entirely the twigs and buds of willow (*Salix* spp.), Rock Ptarmigan largely resin and dwarf birch (*Betula glandulosa* and *B. nana*, which may be conspecific) buds and catkins, and White-tailed Ptarmigan many cones of green alder (*Alnus crispa*) as well as birch and willow (West and Meng 1966; Weeden 1967, 1969; Moss 1973).

Associated with these differences in diet, the ptarmigan have bills and gastroliths of different sizes (Weeden 1969). The present paper shows that they also have guts of different lengths. This is further documentation of the theory that gut length is related to diet (Leopold 1953, Rieck et al. 1971, Gardarsson 1971, Moss 1972, Pendergast and Boag 1973) and gives some insight into the way in which present food habits may have evolved.

METHODS

The work was done during the winter of 1969–70, in parallel with a study on the digestibility of ptarmigan foods (Moss 1973). The methods used to estimate the species composition of the diets and techniques for counting fragments of plant epidermis in the droppings of ptarmigan are described in Moss (1973). Gut lengths were measured as in Moss (1972). Gizzards were weighed including the leathery lining but empty of contents. Birds were aged by the methods described for the three species by Weeden and Watson (1967), West et al. (1968), and Braun (1969). The sampling sites were all in the region called "interior Alaska" by Weeden (1969), who has also described the habitat. Eagle Summit and Harrison Creek are both near Miller House, on the Steese Highway, northeast of Fairbanks. Summit Lake is on the Richardson Highway near Paxson, and Murphy Dome is near Fairbanks.

My samples of females and young birds sometimes weighed less than males and old birds. In such cases gut lengths and gizzard weights were also lower in absolute

TABLE 1

GUT LENGTHS AND BODY WEIGHTS OF PTARMIGAN IN ALASKA[1]

	Combined caeca cm	Small intestine cm	Fresh weight g	Number measured
Willow Ptarmigan				
17 Oct. Harrison Creek	104.5 ± 1.7	82.7 ± 1.0	482 ± 6	24
25 Oct. near Eagle Summit	105.5 ± 1.9	81.3 ± 1.6	505 ± 26	14
23 Jan. Summit Lake	110.9 ± 3.1	81.0 ± 2.5	507 ± 22	7
7–8 Mar. Summit Lake	105.4 ± 1.7	78.6 ± 1.2	499 ± 12	24
Rock Ptarmigan				
18 Oct. Eagle Summit	83.5 ± 0.9	93.0 ± 1.3	439 ± 5	27
17 Oct. Harrison Creek	85.8 ± 2.4	93.9 ± 1.4	426 ± 7	21
26 Dec. Murphy Dome	95.1 ± 2.0	99.7 ± 2.3	418 ± 4	7
11 Jan. Wickersham Dome	95.7 ± 1.8	102.3 ± 1.3	417 ± 8	12
7–8 Mar. Rainbow Mountain	88.6 ± 1.3	97.0 ± 1.5	415 ± 7	23
White-tailed Ptarmigan				
19 Nov. Rainbow Mountain	86.8 ± 2.1	89.6 ± 2.4	355 ± 11	5
20 Dec. Rainbow Mountain	89.7 ± 2.9	91.9 ± 2.1	363 ± 9	12
7–8 Mar. Rainbow Mountain	88.6 ± 1.3	92.0 ± 1.5	369 ± 8	10

[1] ± SE of mean.

terms, but were almost exactly the same when expressed per unit of body weight. The data from different sexes and age classes are therefore combined to simplify presentation; this does not affect the conclusions.

RESULTS

Gut measurements.—Moss (1972) showed that a more digestible and concentrated diet decreased gut length in captive Red Grouse (*Lagopus l.*

TABLE 2

RELATIVE GUT LENGTHS AND GIZZARD WEIGHTS OF PTARMIGAN IN WINTER

	Gut lengths[1] (cm/100 g of body weight)		Gizzards (g fresh weight)		
	Caeca	Small intestines	g/kg of body weight	Mean absolute weight ± SE of mean	Number weighed
Willow Ptarmigan 23 Jan. Summit Lake	22	16	31	15.7 ± 0.56	5
Rock Ptarmigan 11 Jan. Wickersham Dome	23	24–25	23	9.6 ± 0.29	12
White-tailed Ptarmigan 20 Dec. Rainbow Mountain	24–25	25	35	12.6 ± 0.30	13

[1] Based on Table 1.

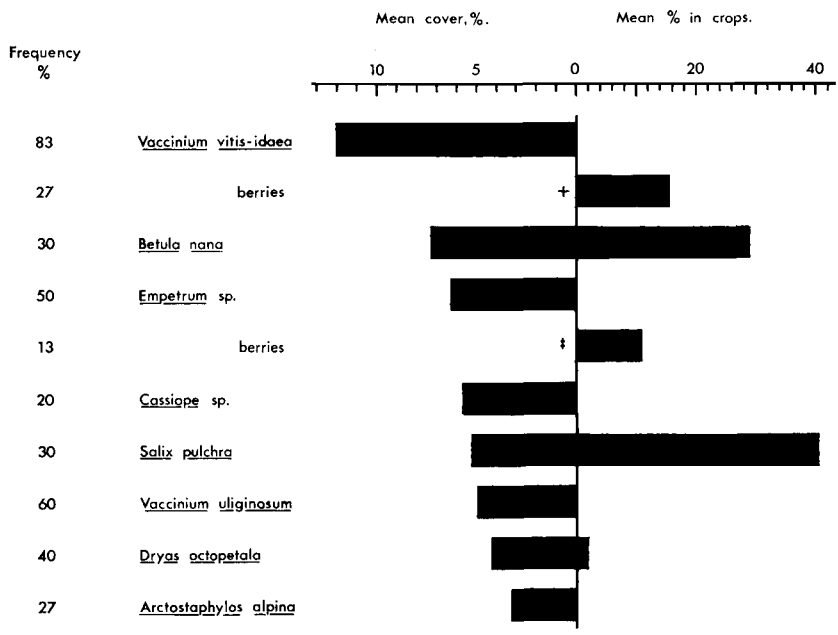

Fig. 1. Foods available to and eaten by series of 26 Rock Ptarmigan shot on 18 October near Eagle Summit. (Note: The frequency is the percentage of crops in which a food item occurred. The cover of each plant species is given as the mean percentage cover in 30 1-m^2 quadrats scattered evenly over the tract where the birds were feeding. Cover within each quadrat was estimated by eye to the nearest 10%. The crop contents are given as the mean percentage of each item by dry weight. Twelve Willow Ptarmigan shot on the same hillside, but lower down, were eating almost entirely willow (98 ± 1%), part of which was *S. pulchra*, + 2.0 berries/sq. m., i.e. 0.0001% cover, ± 0.5/sq. m., i.e. 0.00025% cover.)

scoticus), and thought that the gut length of wild birds should be related to the nature of their diet. The caeca and small intestines of Alaskan Rock Ptarmigan both lengthened from autumn to winter (Table 1) as the birds switched from a diet of berries (27%, mostly *Vaccinium vitis-idaea* and *Empetrum* sp.), willow (41%), and birch (29%), to one almost entirely of birch (percentage data from Fig. 1). No change was detected in the gut lengths of Willow Ptarmigan and their diet did not alter appreciably, being over 90% willow in all the samples in Table 1. These observations confirm that gut length is related to diet.

Different species had different gut measurements. To allow for differences in body weight, the mean gut lengths in Table 1 and the mean gizzard weights were divided by mean body weight (Table 2). The relative lengths of caeca differed little in winter. The main difference was

TABLE 3

CORRELATIONS BETWEEN PERCENTAGE DRY WEIGHT OF FOOD ITEMS IN CROPS OF PTARMIGAN AND PERCENTAGE COUNTS OF EPIDERMAL FRAGMENTS IN THEIR LARGE INTESTINES[1]

		Correlation coefficient	Significance level	Mean percentage weight in crops
Rock Ptarmigan				
18 Oct. 1969 Eagle Summit (sample of 26)	*Carex* spp.	0.586	0.01	0.6
	Dryas octopetala	0.444	0.05	2.0
	Empetrum sp. berries	0.455	0.05	11
White-tailed Ptarmigan				
20 Dec. 1969 Rainbow Mountain (sample of 13)	*Betula glandulosa* twigs only	0.651	0.02	17
Two coefficients from 20 Dec. and 7–8 Mar. 1969 combined	*Betula glandulosa* all birch items	0.424	0.1	45
Rainbow Mountain (total sample 23)	*Alnus crispa*	0.442	0.05	51

[1] One other series of Rock Ptarmigan (21 birds eating 89% birch, Table 4) and one of Willow Ptarmigan (21 birds eating 95% willow, Table 4) were also examined but showed no such correlations.

that Willow Ptarmigan had much shorter small intestines than the other species, even without correcting the data for body weight, and even though they were the heaviest birds. Rock Ptarmigan had much the smallest gizzards.

Gut lengths also showed individual variation within the sample shot from any one flock. The sample of 18 October (Table 1) was the only one containing a large proportion of berries. The caecal lengths of these 26 individual Rock Ptarmigan were inversely related to the proportion of berries in their crops ($r = -0.645$, $P < 0.001$). Berries are highly digestible (Pulliainen et al. 1968, Moss 1973) and contain large amounts of soluble carbohydrates. A diet of berries might therefore be expected to reduce the amount of fiber digested and consequently to reduce caecal length (Moss 1972). In this case, differences in the diet of individuals may have lasted long enough to affect their caecal length. To judge by California Quail (*Lophortyx californicus*), this is likely to be about 2 weeks (Lewin 1963). Alternatively, each individual may have eaten the diet to which its caeca were best adapted. Either alternative implies that food habits, and presumably food preferences, varied consistently among individuals. Such a phenomenon is well-established in laboratory rats (Lát 1967). Further evidence for this tentative suggestion is that the proportions of certain items in the crops were correlated with percent

TABLE 4

EXAMPLES OF WINTER FOOD HABITS OF PTARMIGAN IN THE PRESENCE AND ABSENCE OF THE OTHER SPECIES AT THE TIME OF SHOOTING[1]

	Only one species present			Both other species present		
	Willow	Rock	White-tailed[2]	Willow	Rock	White-tailed[2]
	Summit Lake 23 Jan.	Murphy Dome 26 Dec.	Rainbow Mountain 20 Dec.	Summit Lake 7–8 Mar.	Rainbow Mountain 7–8 Mar.	Rainbow Mountain 7–8 Mar.
Sample size	5	7	13	21	21	10
Willow buds and twigs	97 ± 1	3 ± 2	3 ± 1	95 ± 1	2 ± 1	2 ± 1
Birch buds and catkins	3 ± 1	92 ± 2	30 ± 6	5 ± 1	89 ± 4	41 ± 7
Birch twigs			17 ± 5			2 ± 1
Alder cones			48 ± 6		7 ± 2	56 ± 8

[1] Data expressed as mean percent ± SE of mean.
[2] These two samples of White-tailed Ptarmigan were shot at the same site (where very little willow was present). Snow was less than 1 m deep on 20 December, over 2 m on 7–8 March (see text).

counts of epidermal fragments in the large intestines (Table 3) in Rock and White-tailed Ptarmigan but not Willow Ptarmigan.

Interspecific differences in food preferences.—The three species maintained their distinct diets whether they were alone or in the presence of other species (Table 4). This point is not specifically mentioned by Weeden (1967, 1969) or West and Meng (1966). This is probably because it seems so obvious, at least for Rock and Willow Ptarmigan, which eat almost entirely one food plant in winter. It is of theoretical interest because the separation in winter diets might conceivably be due to direct competition. The evidence suggests that this is not the case, and that each species prefers its own diet.

In 248 autumn crops of Rock Ptarmigan, Weeden (1969) recorded only 11% willow, the rest of the diet being mostly birch (51%) and berries (23%). My 18 October sample of Rock Ptarmigan was eating 41% willow and only 29% birch. This was roughly in proportion to the amounts available (Fig. 1), suggesting that these Rock Ptarmigan found birch and willow equally attractive in autumn. Hence their diet overlapped that of Willow Ptarmigan to some extent. The two species were separated because the Rock Ptarmigan were keeping to higher, more open ground than Willow Ptarmigan, as is generally true in autumn. In winter, when both occupy the same habitats, they eat almost completely different diets. Even when the species of ptarmigan eat one species (birch) or genus (willow) of plant, they reduce overlap in their diets by eating different

TABLE 5

PARTS OF PLANTS EATEN BY ALASKAN PTARMIGAN IN WINTER, PERCENT DRY WEIGHT[1]

	Willow Ptarmigan	Rock Ptarmigan	White-tailed Ptarmigan
Willow			
Large twigs and buds	ca. 90		
Smaller twigs and buds		<10	0–60
Birch			
Catkins and buds	ca. 10[2]	ca. 90	0–50
Twigs	ca. 10[2]		0–20
Alder			
Cones	0	<10	0–80

[1] This table is summarized from West and Meng (1966), Weeden (1967, 1969), and Table 4.
[2] When eating birch, Willow Ptarmigan seem to prefer catkins, then buds, then twigs. Catkins preponderated in the birch eaten by Willow Ptarmigan in Table 4, and there were no birch twigs. Also the data of West and Meng (1966) show that when Willow Ptarmigan ate more than 4% birch in winter, 75% of it was catkins (the authors did not differentiate between buds and twigs).

parts of the plant (Table 5). Another difference is that Willow Ptarmigan often feed while perching off the ground in willow scrub, whereas the other two species feed largely from the ground or the surface of the snow.

White-tailed Ptarmigan in Alaska sometimes take birch twigs, unlike Rock Ptarmigan, which eat almost only buds and catkins (Weeden 1969). At one site favored by White-tailed Ptarmigan, I noticed that the birch scrub was heavily browsed in December and the birds were eating many birch twigs (Table 4). In March, recent heavy snow had made unbrowsed birch higher up the bushes accessible and the birds were eating fewer twigs. Evidently they preferred catkins and buds but took twigs when catkins and buds were scarce at the feeding site, exactly as Rock Ptarmigan do in Iceland. Twigs are probably less nutritious than catkins and buds (Gardarsson and Moss 1970).

Rock and Willow Ptarmigan are more widely distributed than White-tailed Ptarmigan in Alaska (Weeden 1965). Even in parts of Alaska where Rock Ptarmigan do not winter beside White-tailed Ptarmigan, they still eat very little alder (Weeden 1969). So Rock Ptarmigan seem to prefer birch to alder even where no White-tailed Ptarmigan are present to compete with them.

DISCUSSION

Gut lengths.—The evidence in this paper and in Moss (1972) makes it reasonable to assume that gut lengths and gizzard weights are largely determined by diet. The main advantage of large guts is that they can deal with poor quality food containing much fiber and small amounts of nutrients. But small organs make smaller demands on a bird's metab-

olism and weigh less. A bird with the smallest possible gut and gizzard for a given diet will need less food and also be able to fly better. It follows that birds should select the most concentrated food available to them in order to minimize gut and gizzard size.

In fact, different parts of the digestive tract vary independently of each other. The data in this paper allow one to suggest that a diet of willow enables Willow Ptarmigan to exist with shorter intestines than Rock or White-tailed Ptarmigan. A diet of birch seems to require longer intestines than a diet of willow, but it allows Rock Ptarmigan to have their small gizzards, which might make it difficult to survive on willow and alder. A mixed diet of willow, birch, and alder seems to offer the White-tailed Ptarmigan no possibility of a smaller gut or gizzard; but the fact that they have both large guts and large gizzards probably allows them to exploit alder cones and birch twigs that the other Alaskan species do not use much.

What aspects of the diet cause the differences in gut morphology? Moss (1973) suggested that the resins in birch and alder are partly indigestible. Possibly these resins hinder the digestion of protein, like tannins (Feeny 1970). Although all three foods contain similar levels of crude protein (all about 13%, West, pers. comm.) the amount that is actually digestible might therefore be different. In turn, this might partly explain the short intestines of Willow Ptarmigan; they do not eat such resinous material and might therefore extract the required nutrients from their food in a shorter time.

Willow twigs are tough and fibrous to handle but birch catkins and buds are more friable and can be crumbled by hand. Alder cones are harder than birch catkins and buds but not so tough as willow twigs. They are by far the largest of the common food items (typically 5×10 mm); willow twigs are of intermediate size ($1–2 \times 5–10$ mm) while birch catkins and buds are usually small ($1–2 \times 2–3$ mm) with occasional larger catkins (up to 3×10 mm). These observations suggest that willow may require more effort to grind than birch, and cause Willow Ptarmigan to have larger gizzards than Rock Ptarmigan. White-tailed Ptarmigan also have large gizzards; possibly alder cones are also more difficult to grind than birch.

Diets and competition.—In Iceland, only Rock Ptarmigan occur. They have a wider range of winter foods than in Alaska, eating birch (*Betula nana* and *B. pubescens*) twigs and willow (mostly *Salix herbacea* and *S. phylicifolia*) twigs and buds in addition to birch buds and catkins. (No alder grows in Iceland.) Nonetheless, Icelandic ptarmigan prefer willow to birch, usually turning to birch only when willow is unavailable

under deep snow (Gardarsson and Moss 1970, Gardarsson 1971). This suggests that Rock Ptarmigan have adapted to a specialized diet of birch in Alaska in order to avoid competition with Willow Ptarmigan. Such an interpretation is also consistent with the observation that Alaskan Rock Ptarmigan would eat much willow when spatially separate from Willow Ptarmigan in autumn (Fig. 1), as opposed to winter when they ate little willow and the two species of ptarmigan used the same ground.

Rock Ptarmigan in Iceland eat birch twigs when catkins are heavily browsed (Gardarsson and Moss 1970), like White-tailed but unlike Rock Ptarmigan in Alaska. Why do they not eat birch twigs in Alaska? Possibly this would bring them into competition with White-tailed Ptarmigan, which seem to be better adapted to eating twigs because they have larger gizzards.

White-tailed Ptarmigan in Alaska eat some birch and willow buds and catkins and thus presumably endure some competition from the other two species. Why do they not specialize on alder or eat more birch twigs in order to reduce competition? Possibly alder is so poor a food that White-tailed Ptarmigan have found it worth a little competition to maintain an adequate diet. This suggestion is consistent with the observation that White-tailed Ptarmigan have larger gizzards and longer guts than would be expected from a mixed diet of birch buds and catkins and willow, with no alder or birch twigs (Table 2).

In Colorado only White-tailed Ptarmigan occur, and they eat largely willow species during the winter (Weeden 1967, May 1970). This evidence is less useful than the comparison from Iceland as a guide to food preferences, as little else is available in their winter habitat (Weeden 1967, May 1970). I have no measurements of winter gut lengths in Colorado White-tailed Ptarmigan, but predict that they should have shorter small intestines than in Alaska, by analogy with Willow Ptarmigan. This could be tested.

Another interesting comparison would be between Rock Ptarmigan in Iceland and Alaska. The Icelandic birds eat willow and birch twigs, so one would expect them to have larger gizzards (because of both types of twigs) and shorter small intestines (because of the willow) than in Alaska.

ACKNOWLEDGMENTS

I thank D. R. Klein and G. C. West for hospitality and the use of facilities, R. D. Guthrie for allowing me to examine ptarmigan he had shot, R. B. Weeden for advice about study areas, and A. Watson and C. MacInnes for helpful comments on the manuscript. The work in Alaska was supported by the Alaska Cooperative Wildlife Research Unit, the Institute of Arctic Biology and the University of Alaska while I was on leave of absence for a year from the Nature Conservancy in Scotland.

SUMMARY

The three species of ptarmigan in interior Alaska winter in the same areas but have different diets. These diets have different physical and chemical characteristics and are also associated with gross differences in the birds' digestive tracts: Willow Ptarmigan have the shortest small intestines and Rock Ptarmigan the smallest gizzards. These differences in gut morphology are claimed to be among the proximate reasons why each species maintains its separate diet. In Alaska, Rock Ptarmigan prefer birch to willow in winter. In Iceland, only Rock Ptarmigan occur and there they prefer willow to birch. This reversal is attributed to competition with Willow Ptarmigan in Alaska, causing Rock Ptarmigan to adapt to birch.

LITERATURE CITED

BRAUN, C. E. 1969. Population dynamics, habitat, and movements of White-tailed Ptarmigan in Colorado. Unpublished Ph.D. dissertation, Fort Collins, Colorado State Univ.

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.

GARDARSSON, A. 1971. Food ecology and spacing behavior of Rock Ptarmigan (*Lagopus mutus*) in Iceland. Unpublished Ph.D. dissertation, Berkeley, Univ. California.

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, Blackwell Sci. Publ.

LÁT, J. 1967. Nutrition, learning and adaptive capacity. Pp. 169–180 *in* The chemical senses and nutrition (M. R. Kare and O. Maller, Eds.). Baltimore, Johns Hopkins Press.

LEOPOLD, A. S. 1953. Intestinal morphology of gallinaceous birds in relation to food habits. J. Wildl. Mgmt. 17: 197–203.

LEWIN, V. 1963. Reproduction and development of young in a population of California Quail. Condor 65: 249–278.

MAY, T. A. 1970. Seasonal foods of White-tailed Ptarmigan in Colorado. Unpublished M.S. thesis, Fort Collins, Colorado State Univ.

MOSS, R. 1972. Effects of captivity on gut lengths in Red Grouse. J. Wildl. Mgmt. 36: 99–104.

MOSS, R. 1973. The digestion and intake of winter foods by wild ptarmigan in Alaska. Condor 75: 293–301.

PENDERGAST, B. A., AND D. A. BOAG. 1973. Seasonal changes in the internal anatomy of Spruce Grouse in Alberta. Auk 90: 307–317.

PULLIAINEN, E., L. PALOHEIMO, AND L. SYRJALA. 1968. Digestibility of blueberry stems (*Vaccinium myrtillus*) and cowberries (*Vaccinium vitis-idaea*) in the Willow Grouse (*Lagopus lagopus*). Suomal Tiedeakat, Toim. Ser. A, 4, No. 126.

RIECK, C. R., E. S. DZIEDZIC, AND R. G. JEFFREY. 1971. A high density of pheasants at Seattle, Washington. Murrelet 52: 7–9.

WEEDEN, R. B. 1965. Grouse and ptarmigan in Alaska, their ecology and management. Juneau, Alaska Dept. Fish and Game.

WEEDEN, R. B. 1967. Seasonal and geographic variation in the foods of adult White-tailed Ptarmigan. Condor 69: 303–309.

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

WEEDEN, R. B., AND A. WATSON. 1967. Determining the age of Rock Ptarmigan in Alaska and Scotland. J. Wildl. Mgmt. 31: 825–826.

WEST, G. C., AND M. S. MENG. 1966. Nutrition of Willow Ptarmigan in northern Alaska. Auk 83: 603–615.

WEST, G. C., S. SAVAGE, L. IRVING, AND L. J. PEYTON. 1968. Morphological homogeneity of a population of Alaska Willow Ptarmigan. Condor 70: 340–347.

Alaska Cooperative Wildlife Research Unit and Institute of Arctic Biology, University of Alaska, College, Alaska 99701. Present address: Institute of Terrestrial Ecology, Blackhall, Banchory, Kincardineshire AB3 3PS, Scotland. Accepted 15 November 1973.