Regulation and Grinding Ability of Grit in the Gizzard of Norwegian Willow Ptarmigan (*Lagopus Lagopus*)

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ABSTRACT Fluctuations in grit composition in the gizzards of willow ptarmigans and the grinding ability of various grit assortments from wild ptarmigans were examined. We confirmed reports of other investigators that larger, fewer and rounder stones were present in the winter than in the autumn. Experiments showed that ptarmigans prefer stones with diameters between 2-5 mm. Birds on a constant diet maintained a constant stone intake throughout the year. The composition of gizzard grit was influenced by the availability of stones as well as of the type of food the ptarmigans ate. Using an artificial gizzard, grit from birds shot during the autumn was found to be a more efficient grinding material than grit from winter birds. We suggest that other functions than grinding, such as supplying minerals, may be equally important functions of the grit.

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INTRODUCTION

SEVERAL investigators have noted a seasonal fluctuation in quantity, size and angularity of gizzard stones (grit) in Norwegian willow ptarmigans *Lagopus lagopus* (Olstad and Lid, 1923, Kolderup, 1924, Myrberget *et al.*, 1975). Briefly, there are larger, fewer and rounder stones in the winter than in the autumn. It is generally assumed that the grit is important in grinding food and Siivonen (1962) states that lack of grit may be a severe mortality factor in wild ptarmigans during winters with heavy snow. We have investigated the regulation of the grit content and its grinding function.

Specifically, we have raised the following questions: 1) Is the variation in grit content truly seasonal like the change in plumage colour, or is it more connected to availability of grit? 2) Does the ptarmigan regulate the amount and composition of stone intake and excretion according to diet? 3) How efficient are different grit assortments in grinding different types of natural food? These problems have been investigated partly by examination of grit from wild birds and partly by experimental work on captive ptarmigans.

MATERIAL AND METHODS

Grit composition. Gizzards were collected from:

1) Wild ptarmigans shot during the autumn and winter in Troms county, Norway.
2) Captive ptarmigans killed during autumn and winter while on a diet of:
   A) Pellets, grit and water *ad lib.* or,
   B) Simulated winter diet consisting of twigs and buds of willow (*Salix spp.*) and birch (*Betula spp.*) with water and grit *ad lib.*

   The number of birds in each group is shown in Table 2.

The gizzards were opened and the contents mixed with water where the grit sank while the rest of the gizzard material floated off the top. The stones were dried and sized, using standard sieves with hole diameters of 4 mm., 3 mm., 2 mm. and 1 mm. The number of stones in each class was counted.

Regulation of Grit. Experiments were carried out to see if stone intake and excretion were correlated with 1) the amount of grit

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TABLE 1.—*Ptarmigans' diet during grit regulation trials*

Day	Up to day 0	1-8	9-12	13-16	17-22	23-28	29-34
Diet	Birch, willow, pellets	pellets	willow	birch	pellets	willow	birch

TABLE 2.—*Average number and size of gizzard stones in wild ptarmigans during different snow conditions and in captive ptarmigans. n = number of birds*

Time of year	Snow cond. food	n	Avg. # of stones	<2 mm. (%)	2-3 mm. (%)	3-4 mm. (%)	>4 mm. (%)
			Wild ptarmigans				
Sept. Oct. Dec. 1972	No snow	18	134	30	64	35	5
	Natural			(22)	(48)	(26)	(4)
Jan. Feb. Mar. 1973	Snow	25	26	0	3	13	10
	Nat.			(0)	(12)	(50)	(38)
Sept. 1973	No snow	40	195	83	82	26	4
	Nat.			(43)	(42)	(13)	(2)
Dec. 1973	Snow	4	23	2	2	14	5
Feb. 1974	Nat.			(9)	(9)	(61)	(22)
Mar. 1974	No snow	3	48	0	2	17	29
	Nat.			(0)	(4)	(35)	(61)
April 1974	Snow	3	21	0	0	12	9
	Nat.			(0)	0	(57)	(43)
			Captive ptarmigans				
Dec. 1973	Pellets	3	266	147	87	24	7
				(55)	(33)	(9)	(3)
Dec. 1973	Birch willow	4	46	6	8	19	13
				(13)	(17)	(41)	(29)

present in the gizzards and 2) the diet. Four captive ptarmigans, weighing from 490 g. to 585 g., were used in this experiment. Prior to the experiment, they had been kept on a diet consisting of large amounts of birch, some willow, some pellet feed, snow and grit *ad lib.*

At the beginning of the experiment the grit content was increased in two of the birds (#1951, ♂, and #1688, ♂,). They were force-fed 185 (3.8 gms.) and 129 (3.0 gms.) stones, respectively, which had been collected from the gizzard of wild birds shot in late autumn. The other two birds (#1748, ♂ and #1686, ♀) were not force-fed and served as controls. The pairs were placed in separate outdoor cages. Ample grit of known weight and size, ranging from 2 mm. to greater than 5 mm. in diameter, was available to both pairs. The grit containers were constructed to minimize scattering.

The experiment lasted for 34 days and the diet was changed every 3 to 8 days as shown in Table 1. During each willow and birch period small amounts of pellet feed were available to the birds to help keep their weights constant.

At the outset of the experiment and at each change of diet, the stones offered the birds were weighed and sized, and the weight and size composition of stones consumed per day were calculated. All the feces were collected, and the stones separated as described previously. The grit was then dried, sized and weighed. The weight and size composition of grit consumed and excreted per bird per day was calculated for the different diet periods.

Grinding Ability of Grit in an Artificial Gizzard. An artificial gizzard (Fig. 1) was constructed to study grinding ability of typical grit assortments. The gizzard sac was made from the thumb of a rubber glove, closed by tape and placed in a spherical depression. A top plate, with a 500 gram weight, rested

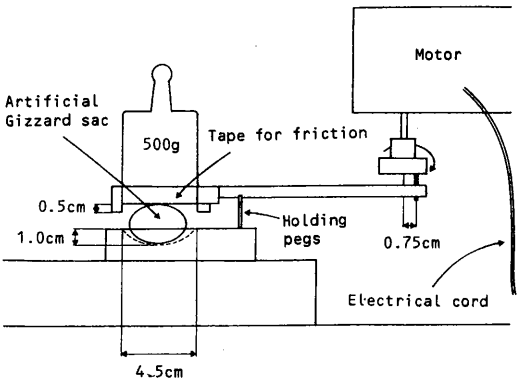

FIG. 1. The artificial gizzard. The gizzard material is contained in a rubber sac and ground by the circular movements of the 500 g. weight.

on the sac and was moved with a circular, horizontal movement, by means of an excentric wheel. This should duplicate the pressure pattern described for turkey gizzards *in situ* (Dziuk and Duke, 1972). The weight which supplied the pressure was chosen to give good grinding in 24 hrs.

The gizzard bag was run for 24 hours at room temperature. Both before and after each trial, the food sample was sized as described for grit. Each size group was weighed and its percentage of the total weight was calculated.

The grit assortments represented extremes: an autumn assortment of 477 stones and a winter assortment of 9 stones. Both of these had been collected from killed wild birds. In addition we measured the grinding effectiveness when no stones were present at all. The autumn grit consisted of 4 stones larger than 4 mm., 28 stones between 3-4, 151 stones between 2-3 and 294 stones smaller than 2 mm. The winter grit consisted of 5 stones larger than 4 mm. and 4 stones between 3 and 4 mm.

Three different diets were tried in the "gizzard": birch buds (*Betula spp.*), willow buds (*Salix pentandra*) and stems of blueberry heather (*Vaccinium myrtillus*). Each of the diets was run at least twice with each of the different grit assortments and without any grit.

RESULTS

Grit Composition. The amount and composition of grit in wild ptarmigan gizzards agrees well with the availability of stones in their environment (Table 3). While the ground was snow-free, the gizzard contained 100-200 stones and about half of them were less than 3 mm. After the snow cover appeared, the number of stones fell to 30 or less. The number of stones less than 2 mm. quickly went to zero, and the number of stones 2-4 mm. in size dropped markedly. Stones greater than 4 mm. showed an increase in absolute number soon after snow cover appeared and thereafter decreased steadily throughout the winter.

At all times of the year, the gizzards of captive birds on pellet food were found to contain a grit assortment similar to that of wild ptarmigans in the autumn, while captive birds on a diet of birch and willow had a grit assortment between an autumn and winter grit assortment of wild birds (Table 2).

Grit Regulation. The two birds that had been force-fed grit always consumed less grit than the control birds (Table 3). On most diets they also excreted less grit. Over the entire experimental period the force-fed birds consumed 3.4 gm. more than they excreted. The difference compares well with the amount force-fed to the birds (3.0 and 3.8 gms.).

Both consumption and excretion of grit was lowest when the birds were on a pellet diet, highest when on birch, and intermediate on willow. The ptarmigans always seemed to prefer stones with diameter above 3 mm., regardless of diet. Stones smaller than 2 mm. were very rarely ingested (Table 3 and 4).

Grinding Ability of Grit in the Artificial Giz-

TABLE 3.—*The amount of stones consumed and excreted per day per bird on three different diets. A = experimental birds (#1951 and #1688). B = control birds (#1686 and #1748)*

Diet	Birds	Consumption per day (grams)	Excretion per day (grams)	Difference Δ con-ex = Δ (grams)
Pellet	A	0.42	0.59	−0.17
	B	0.78	0.38	+0.40
Willow	A	1.96	0.62	+1.34
(Salix spp)	B	—	1.47	—
Birch	A	0.22	0.63	−0.41
(Betula spp)	B	1.91	1.13	+0.78
$Pellet_2$	A	0.14	0.30	−0.16
	B	0.50	0.34	+0.16
$Willow_2$	A	1.11	0.60	+0.51
(Salix spp)	B	1.60	0.43	+1.17
$Birch_2$	A	0.55	0.78	−0.23
(Betula spp)	B	2.22	1.23	+0.99

TABLE 4.—*Composition of stones consumed and excreted per bird per day on different diets. Data from control birds #1748 and #1686. Con = stones consumed. Exc = stones excreted*

Diet		>4 mm. (grams) %	3–4 mm. (grams) %	2–3 mm. (grams) %	<2 mm. (grams) %	Total (grams) %
Pellet feed	Con	(0.86)	(0.20)	(0.30)	(0.00)	1.36
		63	14	23	0	—
	Exc	(0.23)	(0.05)	(0.08)	(0.36)	0.72
		32	7	11	50	—
Willow (*Salix* spp)	Con	(0.89)	(2.26)	(0.02)	(0.00)	3.17
		28	71	1	0	—
	Exc	(0.49)	(0.39)	(0.28)	(0.68)	1.84
		27	21	15	37	—
Birch (*Betula* spp)	Con	(0.69)	(3.95)	(0.00)	(0.00)	4.64
		15	85	0	0	—
	Exc	(0.33)	(0.25)	(0.60)	(1.18)	2.36
		14	11	25	50	—

zard. In all the trials, regardless of diet, the grit assortment from wild ptarmigan shot in autumn was the most effective grinding agent (Fig. 2). Good agreement was found between parallel runs with the same food and the same grit. In most cases, grinding using a winter grit assortment was almost equivalent to grinding using no stones. Birch buds were the most grindable diet.

DISCUSSION

The amount and composition of grit in the gizzards appears to be regulated partly by internal (homeostatic) factors and partly by external (environmental) conditions. Grit consumption depends on the amount of grit already present in the gizzard, and the ptarmigans have a clear preference with regard to the size of grit they consume. This internal regulation does not appear to have an annual cycle since captive birds with constant food and grit available *ad lib.* show steady grit consumption.

Environmental factors like the availability of grit and of various foods, (climatically determined) modify the grit amount and composition. A clear inverse relation was found between snow cover and grit content.

In our experiments the type of food eaten influenced both stone intake and stone excre-

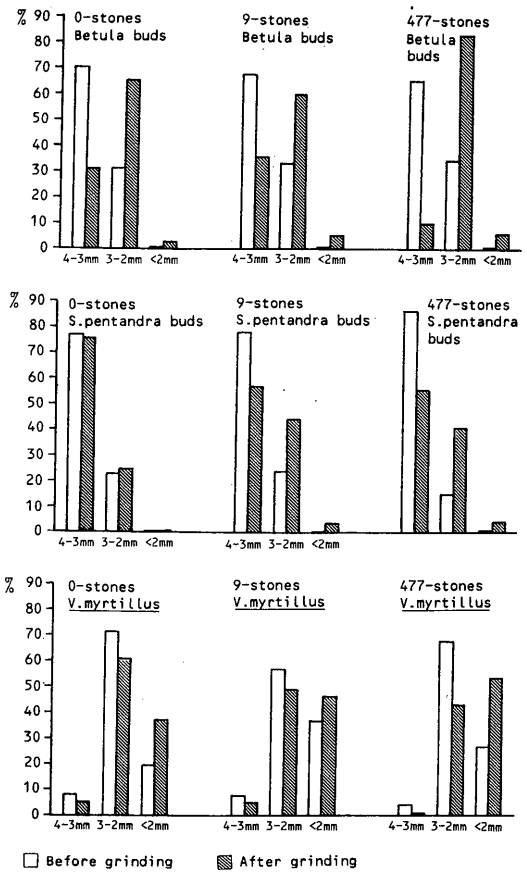

FIG. 2. Shows the percentage of the total weight of birch buds, willow buds and blueberry heather before (open bars) and after (hatched bars) 24 hours of grinding in the artificial gizzard with 3 grit assortments. Data are the averages of all trials.

tion. Ptarmigans fed willow and birch consumed and excreted 2-4 times as many stones as those on pellet food. This is possibly due to the greater coarseness of birch and willow which may cause a high stone excretion which must be replaced by high intake to maintain homeostasis. There must be a considerable degree of stone disintegration in the gizzard since about half of the stones excreted were below 2 mm. This has been shown to be the case in pheasants (Vance, 1971). Tindall (1973) showed that calcareous rocks disintegrate rapidly when shaken in HCl of the same pH as found in the gizzard of ptarmigans.

The results from the artificial gizzard indicate that normal grit from the autumn, when the natural diet consists of berries and other soft material, is a much more efficient grinding agent than that found during the winter when the natural food is tough and really requires efficient grit. In our "gizzard" the winter grit was essentially of no help at all in grinding food. The fact that ptarmigans in good health, but lacking gizzard grit altogether, are frequently shot during the late winter (personal observation), supports the notion that grit is of limited importance in grinding food during the winter. Siivonen's (1962) claim that lack of grit during the winter may be a severe mortality factor in ptarmigans ought to be reinvestigated. It appears likely that stone consumption may be as important as a source of minerals, particularly Ca^{++}, during egg laying and chick development, as for grinding.

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