THE DIGESTION AND INTAKE OF WINTER FOODS BY WILD PTARMIGAN IN ALASKA

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This paper describes a method for measuring the digestibility, metabolizable energy, and daily intake of foods eaten by wild ptarmigan in winter, using the magnesium which occurs naturally in the food as a digestibility marker. This method has already been tested on captive Red Grouse (*Lagopus lagopus scoticus*) (Moss and Parkinson 1972). Further laboratory tests with captive Rock Ptarmigan (*Lagopus mutus*) are now presented together with winter energy budgets of free-living Willow (*Lagopus lagopus*), Rock, and White-tailed (*Lagopus leucurus*) Ptarmigan in Alaska.

METHODS

EXPERIMENTS WITH CAPTIVES

Most of the work on captive birds was done in Scotland during the winter when birds were not molting, laying, or growing. Rock Ptarmigan hatched from eggs collected in the wild in Scotland and reared (Moss 1969) in captivity were used.

For the trials, birds were kept in cubic cages with 60-cm sides and with 1.25-cm mesh wire floors. Droppings fell on to plastic-covered trays and were collected daily. The food eaten and droppings produced each day were weighed fresh and the moisture content of samples determined at 100°C. Magnesium was estimated by atomic absorption spectrophotometry.

To test the validity of the magnesium marker method, captive Rock Ptarmigan were fed several widely different foods (table 1). In each trial, the birds were fed their usual pellets (Grouse Maintenance pellets, Northern Agricultural and Lime Company, 30 Waterloo Quay, Aberdeen AB9 8DN, Scotland) for a week or so until accustomed to their cages. An increasing proportion of the test food was then included in the diet over 10 days, until they were eating nothing else. After a preliminary 5 days on this diet, droppings were collected and food intake measured for a further 5 days. Apparent digestibility (table 1) was measured by two methods, directly (A):

$$A = 100\left(\frac{F-D}{F}\right) \qquad (1)$$

where F is the dry weight of food eaten, and D the dry weight of droppings excreted, and indirectly (A'):

$$A' = 100\left(1 - \frac{M_f}{M_d}\right) \qquad (2)$$

where M_f is the percentage of magnesium in the food and M_d that in the droppings.

In principle, it should be possible to use any mineral element as a marker for digestibility studies in birds, as long as they are in balance for that element. This is because they excrete their solid urine along with the feces, unlike mammals which lose a proportion of each element in their liquid urine. Reasons for preferring magnesium to other elements are given by Moss and Parkinson (1972).

Tetraonids excrete soft, pultaceous "cecal" droppings and hard, fibrous "woody" droppings. The value of M_d in equation (2) may be either the magnesium content of the combined droppings or else the mean of the magnesium content of the two kinds of droppings, weighted in proportion to the relative amounts excreted, i.e.:

$$A' = 100\left(1 - \frac{M_f}{kM_c + (1-k)M_w}\right) \qquad (3)$$

where M_c is the percentage of magnesium in the cecal droppings, M_w that in the woody droppings, and k the proportion of the total formed by the cecal droppings.

To calculate the daily food intake of wild birds from the weight of roost heaps it was necessary to know the relative rate of production of woody droppings during the day and at night (equations 5, 6 below). This was studied indoors, using two cock and two hen Rock Ptarmigan eating a pelleted diet. Light was artificial and daylengths from 5–10 hr were provided. Dusk was mimicked by reducing light intensity half an hour before the lights were switched off, to allow the birds to fill their crops in readiness for the night. After a preliminary 10 days, droppings were collected twice daily at the times when the lights were turned on and off; cecal and woody droppings were weighed separately after drying at 100°C. Collections were continued until three successive running means of the ratio of the weight of droppings produced at "night" and during the "day" agreed to within 5%. This usually took about 10 days (table 2). Food intake was also measured daily.

MEASUREMENTS ON WILD BIRDS

Apparent digestibility (A') could have been calculated using equation (3) if the diets had consisted entirely of one food. However, even the simplest diets usually contained a small proportion of a second food and some diets were more complex. Thus M_f in equation (3) was replaced by the expression

$$M_f = \Sigma\, M_n B_n \qquad (4)$$

where B_n is the proportion of item n in the diet and M_n the percentage of magnesium in item n.

I could have assumed that the species composition of the diet forming a given set of droppings was the same as the crop contents of birds shot nearby (table 3). However, this assumption was unjustifiable where birds were feeding on more than one main food. Instead, the diet was calculated from counts of "epi-

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TABLE 1. The digestion of some foods by individual Rock Ptarmigan in the laboratory.

Food	Sex	Apparent digestibility, % (dry basis) Direct measure-ment	Magnesium marker method
Bulbils of *Polygonum viviparum* (Iceland)	♀	50	50
	♂	51	51
	♂	50	47
Berries of *Vaccinium myrtillus* (Scotland)	♂	62	60
	♀	60	60
Berries of *Empetrum* sp. (Iceland)	♂	47	49
	♂	49	49
	♂	50	50
Catkins of *Betula pubescens* (Iceland)	♂	19	19
Grouse maintenance pellets	♀	51	52

TABLE 2. Rate of production of woody droppings by four captive Rock Ptarmigan in Scotland.

Hours of day-light	Dry weight of droppings produced (g/10 hr) Day Mean (range)	Night Mean (range)	Day/night (T) Mean (range)
5	7.07(6.04–8.04)	4.03(3.94–4.67)	1.76(1.53–1.91)
6	7.05(5.95–7.93)	3.99(3.07–4.53)	1.82(1.42–2.18)
8	6.03(4.82–7.30)	3.49(2.95–3.93)	1.73(1.36–1.95)
10	5.73(5.00–6.79)	3.89(3.34–4.24)	1.49(1.27–1.69)

dermal fragments" of food plants in the droppings (table 4). These fragments are pieces of the plant's epidermis. The epidermal cells of each plant had distinctive outlines which could be distinguished under the microscope after chemical clarification. Factors for converting counts of such fragments to the percentage composition of the diet were calculated by comparing the percentage composition of the crop contents with counts of epidermal fragments made on samples taken from the last few centimeters of the large intestines of the same birds (table 5). Crop contents and intestinal samples from the same group of birds were assumed to represent the same diet. These conversion factors were then used to calculate the diet from the droppings (Appendix A).

The daily output of droppings (S) was calculated from the mean weight of a group of roost heaps (R), the time spent roosting in hours (Z), and the ratio of the rate of production of woody droppings during the day to that at night (T).

$$S = \left(R + \frac{TR(24-Z)}{Z}\right)\frac{1}{1-k} \qquad (5)$$

Z was assumed to be the same as the inactive period recorded by West (1968) for Willow Ptarmigan in Fairbanks. A correction for latitude was made by subtracting from Z the difference in nautical day-length between Fairbanks and the sampling site. A value of T appropriate to each Z was taken from table 2.

TABLE 3. Crop contents of ptarmigan (mean % dry weight ± standard error of the mean).

	Willow Ptarmigan 7–8 March[a]	Rock Ptarmigan 18 Oct[b]	Rock Ptarmigan 7–8 March[a]	White-tailed Ptarmigan 20 Dec[c]	White-tailed Ptarmigan 7–8 March[a]
Salix spp.					
Buds and twigs	95 ± 1	41 ± 4	1.6 ± 0.8	2.6 ± 0.5	
Betula glandulosa					
Buds and small catkins	5 ± 1	29 ± 3	19 ± 3	30 ± 6	33 ± 7
Large catkins			70 ± 4		7 ± 2
Twigs				17 ± 5	2.4 ± 0.6
Alnus crispa					
Cones			7 ± 2	10.8 ± 4.6	56 ± 8
Sample size	(21)	(26)	(21)	(13)	(10)

[a] Summit Lake, near Paxson, Richardson Highway.
[b] Eagle Summit, near Miller House, Steese Highway. Other major items included *Vaccinium vitis-idaea* berries (16 ± 2%) and *Empetrum* sp. berries (11 ± 1%). The table omits some minor foods.
[c] Rainbow Mountain, near Paxson.

TABLE 4. Epidermal fragments of food plants in the large intestines of ptarmigan (mean % of identified items ± standard error of mean).[a]

	Willow Ptarmigan 7–8 March	Rock Ptarmigan 18 Oct	Rock Ptarmigan 7–8 March	White-tailed Ptarmigan 20 Dec	White-tailed Ptarmigan 7–8 March
Salix spp.	82 ± 1	65 ± 3	1.6 ± 0.5	2.6 ± 0.5	
Betula glandulosa	18 ± 1	29 ± 2	96 ± 1	74 ± 1	94 ± 1
Alnus crispa Cones			1.0 ± 0.4	7 ± 1	4.8 ± 0.7

[a] These data are from the same birds as in table 3.

TABLE 5. Factors (F)[a] for converting counts of epidermal fragments of ptarmigan food plants in the droppings into percentage intakes.[b]

	Willow Ptarmigan 7–8 March	Rock Ptarmigan 18 Oct	Rock Ptarmigan 7–8 March	White-tailed Ptarmigan 20 Dec	White-tailed Ptarmigan 7–8 March
Salix spp.	1.00 ± 0.02	1.00 ± 0.14	1.06 ± 1.34	0.95 ± 0.51	
Betula glandulosa	0.22 ± 0.10	1.64 ± 0.56	1.00 ± 0.05	1.00 ± 0.16	1.00 ± 0.17
Alnus crispa			8.3 ± 6.2	10.8 ± 4.6	25.4 ± 6.9

[a] The error estimate of each F was calculated by logarithmic differentiation using the standard error of the mean of each contributory measurement as a basis (see Appendix A).
[b] These data are from the same birds as in tables 3 and 4.

Daily food intake (I) was given by

$$I = 100\frac{S}{100 - A'} \quad (6)$$

and metabolizable energy (E) by

$$E = \Sigma C_n B_n \left[1 - \frac{\Sigma M_n B_n (kC_c + (1-k)C_w)}{\Sigma C_n B_n (kM_c + (1-k)M_w)} \right] \quad (7)$$

where C_n is the calorific value of item n in the diet, C_w that of woody droppings, and C_c of the cecal droppings.

All samples from the field were taken in "interior Alaska" (Weeden 1968) in the winter 1969–70. In the field, a flock of ptarmigan was sought out. They were known to have been in the same area for several days from signs in the snow and from direct observation. Some were shot and soon froze in the cold air. In the laboratory, the birds were sexed, aged, and weighed (Weeden and Watson 1967; Braun 1969; West et al. 1968). Crop contents were removed, separated into classes of different items, dried to constant weight at 100°C, and weighed. The contents of the last few centimeters of the large intestine were kept for analyzing plant epidermal fragments. Fresh samples of both woody and cecal droppings were collected where the birds were shot, including entire roost heaps. The droppings were already frozen when collected and were kept frozen until required. In the laboratory, the sample was thawed, mixed until homogeneous, weighed, and then three subsamples were taken for determining dry weight at 100°C, chemical analysis for magnesium, and counts of plant epidermal fragments.

The mean magnesium content of food samples picked by hand was sometimes significantly lower than in samples from the crops. Presumably, I must have picked material different from that chosen by the birds. It was therefore not possible to estimate digestibility from hand-picked samples of food in places where droppings were collected but no birds shot, although this had been my intention.

The amount of cecal droppings as a proportion of the total excreta was measured over 24 hr on 13–14 January (17%) and 48 hr on 14–16 January (18%) in Alaska, using four captive Rock Ptarmigan in the same cage on an artificial diet. The proportion for Red Grouse, a subspecies of Willow Ptarmigan, on a natural diet of heather (*Calluna vulgaris*) was 12% (Moss and Parkinson 1972). In the daylength experiments in this paper, the proportion for Scottish Rock Ptarmigan was 11%. For this paper, it was assumed that the proportion of cecal droppings was 15%.

Differences in measured digestibility between the different foods may have been due to differences in the foods, or differences in digestion between different species of ptarmigan. To distinguish these possibilities, five replicates of each of the three main winter foods (willow, birch, and alder, tables 3 and 8) were digested by a standard method (Tilley and Terry 1963) in vitro, using rumen liquor from a fistulated reindeer (*Rangifer tarandus*) which was eating alfalfa pellets.

Gross energy values (table 6) were determined in an adiabatic bomb calorimeter.

TABLE 6. Calorific values of crop contents and droppings, kcal/g dry weight, mean ± range/2 (sample size).

	Willow Ptarmigan Summit Lake 23 Jan	Rock Ptarmigan Eagle Summit 18 Oct	Murphy Dome 26 Dec	White-tailed Ptarmigan Rainbow Mt. 20 Dec
Salix spp.				
Buds and twigs	5.13 ± 0.04 (3)	4.97 ± 0.07 (4)		
Betula glandulosa				
Buds and catkins		5.83 ± 0.01 (2)	5.94 ± 0.07 (3)	5.82 ± 0.04 (3)
Twigs				5.91 ± 0.03 (2)
Alnus crispa				
Catkins				5.42 ± 0.02 (3)
Vaccinium vitis-idaea				
Berries		4.86 ± 0.06 (2)		
Empetrum sp.				
Berries		4.86 ± 0.03 (2)		
Woody droppings	5.21 ± 0.08 (2)	4.53 ± 0.18 (5)	5.41 ± 0.04 (3)	5.11 ± 0.07 (3)
Cecal droppings	5.01 ± 0.03 (3)	5.88 ± 0.08 (2)	7.08 ± 0.11 (3)	6.73 ± 0.14 (3)

TABLE 7. Magnesium in crop contents and droppings of ptarmigan, % dry weight, mean ± standard error of mean (sample size).[a]

	Rock Ptarmigan Eagle Summit 18 Oct	Murphy Dome 26 Dec	White-tailed Ptarmigan Rainbow Mt. 20 Dec	Willow Ptarmigan Summit Lake 23–25 Jan
Salix spp.				
Buds and twigs	0.160 ± 0.004 (17)	0.185 (1)	0.131 ± 0.006 (2)	0.171 ± 0.004 (5)
Betula glandulosa				
Buds and catkins	0.172 ± 0.004 (15)	0.160 ± 0.003 (17)	0.150 ± 0.003 (7)	0.179 (1)
Twigs			0.119 ± 0.003 (5)	
Alnus crispa				
Catkins			0.187 ± 0.007 (5)	
Vaccinium vitus-idaea				
Berries	0.058 ± 0.003 (13)	0.058 ± 0 (2)		
Empetrum sp.				
Berries	0.048 ± 0.003 (14)			
Intestinal droppings	0.201 ± 0.009 (8)	0.268 ± 0.013 (11)	0.302 ± 0.010[b](19)	0.277 ± 0.005 (14)
Cecal droppings	0.209 ± 0.005 (3)	0.174 ± 0.007 (14)	0.134 ± 0.007 (13)	0.485 ± 0.026 (7)

[a] This table omits some determinations which were made on minor foods.
[b] Residual standard error left after removing variation accounted for by regression of % Mg on % alder fragments.

RESULTS

DIGESTIBILITY AND ERRORS

In the laboratory, there was good agreement between the direct measurements of apparent digestibility, and the indirect method using magnesium as a marker (table 1). It therefore seemed reasonable to apply the indirect method to wild birds.

To do this, estimates of the magnesium content of the diet and of the droppings were required. The magnesium content of the individual constituents of the diet and of the two kinds of droppings could be measured with reasonable precision (table 7). The main possible errors in the measures of digestibility (table 8) were in estimating the species composition of the diet and the proportions of the two kinds of droppings (table 9).

TABLE 8. Digestibility and metabolizable energy of winter diets eaten by ptarmigan (dry basis).

Ptarmigan	Diet calculated from droppings and (that in crops[a]) % willow	% birch	% alder	Digestibility, %	Metabolizable energy, kcal/g
Willow					
Summit Lake 23 Jan	95(97)	5(3)	0(0)	44(44)	2.3(2.3)
Rock[b]					
Murphy Dome 26 Dec	1(3)	98(92)	1(0.1)	37(39)	2.3(2.4)
White-tailed					
Rainbow Mt. 20 Dec	5(3)	66(47)	29(48)	45(41)	2.7(2.5)

[a] Digestibility and metabolizable energy values in parentheses were derived by assuming the crop contents of birds shot nearby to represent the diet, instead of calculating it from the droppings.
[b] 5% *Vaccinium vitis-idaea* berries in crops.

Willow Ptarmigan in winter ate mostly willow and Rock Ptarmigan, mostly birch (tables 3 and 8). The magnesium marker technique provided acceptably precise estimates of the digestibility of these simple diets (44% and 37%, tables 8 and 9). The diet of Rock Ptarmigan was 98% birch (table 8); even allowing for large variations in the digestibility of the remaining 2%, birch was also 37% digestible. The diet of Willow Ptarmigan was 95% willow and 5% birch; assuming the birch to be 37% digestible meant that the willow was 45% digestible. This agrees exactly with the estimate of West (1968).

White-tailed Ptarmigan ate a more complex diet of birch and alder, with some willow (tables 3 and 8). Even so, considerable latitude in estimating the composition of the diet was possible with little effect on its calculated digestibility (tables 8 and 9). This was be-

TABLE 9. Possible errors in calculated % digestibilities of ptarmigan diets.

Source of error	Percentage error Willow	Rock	White-tailed
Twofold error in estimating proportions of minor components in diet	0.5	0.5	5.0
Mg in each component of diet in error by 1 SE	1.5	1.0	2.0
Mg in both kinds of droppings in error by 1 SE	1.5	3.0	2.0
Proportion of cecal droppings in error by 5%	2.0	2.5	3.0

The probability of all these errors acting in the same direction is $0.5^5 = 0.003$. It is also unlikely that all the errors would be as large as assumed in this table. SE is the standard error of the mean.

TABLE 10. Weights of roost heaps and calculated daily intakes of food and metabolizable energy by ptarmigan.

Ptarmigan	Date and area	Roost heap g dry wt ± SE (sample size)	Roost period, hr	Value of T used (from table 2)	Food intake g dry wt/day	Metabolizable energy intake kcal/day
Willow	Summit Lake, 23–25 Jan	19.3 ± 0.4 (13)	15.7	1.7	61	140
	Rainbow Mt. 19 Nov	21.3 ± 0.8 (17)	15.0	1.6	70	160
Rock[a]	Rainbow Mt. 20 Nov	14.8 ± 0.4 (9)	15.0	1.6	43	100
	Murphy Dome 20 Feb	13.4 ± 1.0 (3)	13.3	1.5	44	100
White-tailed	Rainbow Mt. 20 Dec	13.9 ± 0.6 (10)	18.0	1.8	39	105

[a] Roost heaps were collected on 26 December and used for determining digestibility (table 6), but the birds had moved about during the night and the weights are therefore not used here.

cause the magnesium content of all constituents was fairly similar (table 7). The digestibility of alder could, in theory, have been calculated from the known digestibilities of willow, birch, and the total diet. However, this calculation was sensitive to small changes in the species composition of the diet and therefore unreliable.

METABOLIZABLE ENERGY AND FOOD INTAKE

The metabolizable energy of the diets of Willow Ptarmigan, Rock Ptarmigan, and White-tailed Ptarmigan was 2.3, 2.3, and 2.7 kcal/g, respectively (table 8). Willow and birch calculated separately also contained 2.3 kcal/g metabolizable energy. A reliable separate estimate for alder cannot be made for the reasons outlined above. Nonetheless, it would seem to be greater than both willow and birch because the diet containing alder also contained the most metabolizable energy.

Daily metabolizable energy intakes were 150, 100, and 105 kcal/day for Willow, Rock, and White-tailed Ptarmigan, respectively (table 10). This value for Willow Ptarmigan is in excess of the figure for captives (117 kcal/day) measured by West (1968) presumably because it includes the "cost of free living" (Kendeigh 1970).

Although birch was less digestible (37%) than willow (45%), its metabolizable energy was the same (2.3 kcal/g; table 8). This was partly due to the high calorific value of birch (5.94 kcal/g) relative to willow (5.13 kcal/g); also, the woody droppings of Rock Ptarmigan contained less energy than the food, while food and woody droppings were fairly similar in Willow Ptarmigan (table 6). The small amount of chloroform-diethyl ether extract in winter willow (4–10%, G. C. West, pers. comm.) compared with birch (30–40%, G. C. West, pers. comm.) would account for the difference in calorific value if the chloroform-diethyl ether extract was fatty or resinous material with a calorific value of about 9 kcal/g.

However, it seems that not all the chloroform-diethyl ether extract in birch is digestible fat. This is suggested by the remarkably high (7.08 kcal/g) energy content of the cecal droppings of Rock Ptarmigan on a diet of birch. It may be inferred that the cecal droppings contain a large proportion of undigested fatty or resinous material of high calorific value. Willow is not notably resinous, whereas both birch and alder are.

The calorific value of alder cones was 5.42 kcal/g (table 6), intermediate between willow and birch. This corresponded with measurements of chloroform-diethyl ether extract of alder (13–20%, G. C. West, pers. comm.) which were also intermediate. As with the Rock Ptarmigan in winter, the woody droppings of White-tailed Ptarmigan contained less energy than the food. Similarly also, the gross energy content of the cecal droppings (6.73 kcal/g) was much higher than that of the food, presumably again due to a large proportion of fatty or resinous material.

EPIDERMAL FRAGMENT COUNTS AND IN VITRO DIGESTIBILITIES

The diet was calculated from counts of epidermal fragments in samples of the droppings used for magnesium determination. However, this technique had severe limitations because conversion factors varied on different occasions (table 5). This could be explained by suggesting that crop material which had been classified into one category (e.g., "birch") could actually be quite different on different occasions (e.g., catkins or twigs). Thus a given set of conversion factors applied only to food items of precisely the same character (see Appendix B).

The difference in digestibility between willow and birch could have been due to differences in the digestive processes of Willow and Rock Ptarmigan rather than in the foods they ate. However, in vitro digestibilities for birch, willow, and alder were 27%, 32%, and 33%, respectively. This indicated that the difference between the digestibility of willow and birch was at least partly due to differences in the foods rather than the birds.

DISCUSSION

SPECIES COMPOSITION OF DIETS

It would have made little difference to the results in table 8 if I had used the crop contents of the shot birds to estimate the diet rather than counts of epidermal fragments in the droppings. For Rock and Willow Ptarmigan this was largely because they ate mostly one food item—birch and willow, respectively. For White-tailed Ptarmigan the reason was that the two main food items, birch and alder, contained fairly similar concentrations of magnesium. Hence, quite large errors in estimating the species composition of the diet could be tolerated with little effect on its estimated digestibility.

This was not true for the mixed October diet of Rock Ptarmigan, which included berries with a low magnesium content relative to birch and willow (tables 5 and 7). Here, a relatively small error in the species composition of the diet would have caused a large error in digestibility. In this case, the diet was not determined from the droppings and the digestibility calculated using the crop contents as an estimate of the diet was 33%. This is markedly different from the digestibility of 48% which I calculated using the diet in table 3, the digestibilities for the major components in tables 1 and 8 plus 81% for *Vaccinium vitis-idaea* berries (Pulliainen et al. 1968). This discrepancy emphasizes the importance of checking the diet by examination of the droppings.

ENERGY BUDGETS

The "existence metabolism" energy requirement measured by West (1968), using closely caged Willow Ptarmigan on an artificial diet, was 117 kcal/day. This is lower than the estimate in table 10 by about 30 kcal/day. I shall refer to this difference as the "cost of free living" (Kendeigh 1970).

Kendeigh (1970) has indicated that the existence metabolism of all birds varies as $W^{0.53}$ at 0°C (where W = live weight), or $W^{0.5}$ for our present purposes. Existence metabolism increases as temperature falls, but this increase is due to changes in thermal conductance which also varies as $W^{0.5}$ at all temperatures below 0°C (Lasiewski and Dawson 1967), though the constant of proportionality may vary with temperature. Expressed on this basis, the existence metabolism of a 500-g Willow Ptarmigan in winter in interior Alaska is 5.2 kcal/day/$W^{0.5}$. Applying this figure to White-tailed Ptarmigan (360 g), existence metabolism should be 100 kcal/day. The cost of free living is therefore 5 kcal/day (table 9), which is less than experimental error and therefore negligible. For Rock Ptarmigan (420 g), existence metabolism is calculated to be 105 kcal/day and the cost of free living is again negligible (table 9). In other words, the cost of free living is estimated to be about 20% of the total energy budget in Willow Ptarmigan, but negligible in Rock Ptarmigan and White-tailed Ptarmigan.

Two possible reasons for the greater energy requirements of Willow Ptarmigan are that willow twigs are particularly tough and difficult to pluck (at least by humans) and that Willow Ptarmigan often feed perched in the branches of willow scrub, a more exposed position than the other two species which feed from ground or snow level.

These estimates of the cost of free living are lower than the results of Drinnan (1958), who estimated that free-living European Oystercatchers (*Haematopus ostralegus*) in Britain ate about half as much again as captive birds. Schartz and Zimmerman (1971) estimated the cost of free living in breeding male Dickcissels (*Spiza americana*) to be about 30% of the energy budget.

However, the present results are in accord with work on Red Grouse. C. J. Savory (unpubl. data) estimated the daily intake of heather by wild Red Grouse to be 50–60 g/day during the winter. Moss and Parkinson (1972) found that captive Red Grouse confined on a small patch of heather (*Calluna vulgaris*) sward ate 60–80 g/day. There was therefore no cost of free living in this case. This is not incompatible with the estimates for Oystercatchers and Dickcissels because Oystercatchers spend much of the day and part of the night feeding, while the measurements on Dickcissels included territorial behavior and other breeding activities. Tetraonids, on the other hand, are not very active during the winter; they spend little time feeding and in

Alaska pass much of the day and all night roosting in snow holes.

FUTURE USE OF METHOD

The magnesium marker technique for measuring digestibility works well on samples taken in the field, and there is no reason why it should not be more generally applied. Its use will be limited to periods when birds are not growing, molting, or laying until the daily magnesium requirements of these processes are known and suitable corrections can be made for retention of magnesium by the bird.

SUMMARY

An indirect technique for measuring the digestibility of foods of ptarmigan is described, using the magnesium which occurs naturally in the foods as a digestibility marker. The method was tested in the laboratory and then applied to three species of ptarmigan in the field. It was essential to use the crop contents for estimating the magnesium content of the diet. Hand-picked samples of foods could not be used because they sometimes contained less magnesium than the same food in the crops. Daily food intakes and energy budgets were calculated by weighing heaps of woody droppings left by birds roosting for known periods.

The technique for measuring digestibility was simple and precise when applied to two diets consisting mainly of one food. A third diet included two major foods; the magnesium content of each food was fairly similar and so a fairly large error in estimating the proportions of the two foods in the diet could be tolerated with little effect on the result. In a fourth case, the magnesium content of two of the four major foods was markedly different from the other two, and in this case a relatively small error in estimating the species composition of the diet would have led to appreciable error in its calculated digestibility.

Factors for calculating the species composition of diets from counts of epidermal fragments of plants in the droppings were derived. This was done by comparing the crop contents with counts of plant epidermal fragments in samples from the large intestine. These factors had to be used carefully because they differed on different occasions. This was when the nature of materials classified under one heading differed, e.g., "birch" might be twigs on one occasion and catkins on another.

The winter energy budgets of free-living ptarmigan were compared with earlier work on captive Willow Ptarmigan. The "cost of free-living" was about 20% of the daily energy budget of Willow Ptarmigan but negligible for Rock and White-tailed Ptarmigan.

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APPENDIX A

This appendix describes the method for estimating the diet from epidermal fragments in the droppings.

Sparks and Malechek (1968) have shown that particle counts of epidermal fragments are an accurate means of determining the dry-weight composition of a mixture of plant materials. Samples from large intestines and samples of droppings were analyzed for epidermal fragments, using a quantitative modification of the method of Baumgartner and Martin (1939).

A sample of droppings was cleared in Hertwig's solution (26 ml HCl, 280 ml water, 110 ml glycerine, 500 ml chloral hydrate crystals) by soaking at room temperature (21°C) for 48 hr or more, and washed through two sieves of square mesh opening 500 and 125 μ. Subsamples of the material retained by the smaller sieve were suspended in water on a covered microscope slide and examined at a magnification of 100×.

All the epidermal fragments in a series of fields were counted on each slide until the count reached about 100. Fragments were classified into cell types. Most of these were assigned to species by reference to specimen slides made from the epidermis of known plants mounted in gum chloral. Several slides were examined until two successive running means of the percentage of each item were closely comparable.

The running mean R was calculated

$$R = \Sigma Y_m / N \qquad (8)$$

where Y_m is the per cent count of item m on a slide and N is the number of slides. The most complex diet examined was that of Rock Ptarmigan in October (table 3). In this case five slides gave running means which changed little with extra slides. Fewer slides were required with simpler diets. It was assumed that the crop contents (table 3) and the intestinal samples (table 4) from the same flock of birds both represented the same diet. Conversion factors were calculated for use in estimating the percentage composition of an unknown diet from fragments in the droppings (table 5).

The main item in the droppings was selected as a reference substance and mean weights or counts of other items expressed as a proportion of the mean weight or count of this item, thus:

$$X_r/X_r : X_1/X_r : X_2/X_r : \ldots X_n/X_r \qquad (9)$$

and

$$Y_r/Y_r : Y_1/Y_r : Y_2/Y_r : \ldots Y_n/Y_r \qquad (10)$$

were calculated to give

$$1 : X'_1 : X'_2 : \ldots X'_n \qquad (11)$$

and

$$1 : Y'_1 : Y'_2 : \ldots Y'_n \qquad (12)$$

then

$$F_n = X'_n / Y'_n \qquad (13)$$

where X_n (or Y_n) and X_r (or Y_r) are the mean per cent weights (or counts) of item n and the reference item r in the crops (or samples from the large intestines) and F_n is the conversion factor for item n. F_n is used to calculate the proportion of n in an unknown diet from epidermal fragments in the droppings thus:

say, the unknown diet gives counts

$$Z_r : Z_1 : Z_2 : \ldots Z_n \qquad (14)$$

divide throughout by Z_r to give

$$1 : Z'_1 : Z'_2 : \ldots Z'_n \qquad (15)$$

then the weight of item n in the diet as a proportion of item r is given by

$$F_n Z'_n \qquad (16)$$

and

$$\% n = \frac{F_n Z'_n}{1 + F_n Z'_n} \times 100 \qquad (17)$$

where $\% n$ is the percentage by weight of item n in the diet.

APPENDIX B

This appendix offers an explanation of the discrepancies between values of F for the same plant species determined on different occasions (table 5).

For White-tailed Ptarmigan, birch was used as a reference substance (Appendix A) in both series and its value of F was therefore unity. Values of F for alder for 20 December and 7–8 March were 10.8 and 25.4, respectively (table 3).

This change in F was associated with a marked difference in the crop material classified as "birch." On 20 December this included a considerable proportion of twigs (34%), the remainder being small buds and catkins (table 3). By contrast, the birch of 7–8 March included relatively few twigs and was mostly large catkins (83%). The alder was all cones of similar appearance on both occasions. The discrepancy in the two values of F for alder would be explicable if the large catkins of birch gave rise to more identifiable fragments/unit weight than the twigs and/or the small catkins and buds.

There was also a large difference between values of F for birch for Rock Ptarmigan on 18 October (1.64) and Willow Ptarmigan on 7–8 March (0.22; table 4). Both the "willow" and the "birch" eaten by these two species differed markedly. Willow Ptarmigan ate mostly catkins of birch with few buds, while Rock Ptarmigan ate a mixture of both catkins and buds. Rock Ptarmigan ate smaller pieces of willow than Willow Ptarmigan. These differences could have caused the discrepancy between the values of F; an alternative (but not exclusive) explanation is that Willow Ptarmigan digested birch (or willow) less (or more) efficiently than Rock Ptarmigan.

The practical result is that conversion factors must be determined anew for each set of circumstances under which they are to be used.