THE DIGESTION OF HEATHER BY RED GROUSE DURING THE SPRING

ROBERT MOSS

Red Grouse (*Lagopus lagopus scoticus*) feed largely on heather (*Calluna vulgaris*) throughout the year (Jenkins et al. 1963). Heather is a poor food by agricultural standards, containing little protein (50–100 g/kg) and phosphorus (0.5–1 g/kg) and much crude fibre (about 250 g/kg).

The breeding performance and breeding densities of Red Grouse are thought to be related to their plane of nutrition (Watson and Moss 1972). The critical season is spring (Moss et al. 1975), when the hens are laying their eggs. In this study I measured nutrient and energy balances in spring in order to improve our understanding of the hens' nutrition at this time.

During the work it became apparent that free-living wild grouse digested heather much more efficiently than the captives studied previously by Moss and Parkinson (1972). A secondary aim of this report is to document that difference.

METHODS

MEASUREMENTS ON CAPTIVE HENS

Four hen Red Grouse from captive stock were kept in the open in roofed cubic cages with 60 cm sides and with 1.25 cm mesh wire floors. Droppings fell onto plastic-covered trays and were collected twice weekly from 3 April 1972 until the birds had either finished laying or until they had laid ten eggs, whichever was the sooner. The last collection was on 22 May. Droppings were frozen at –15° until they were freeze-dried and then milled to pass through a 1 mm mesh sieve. No attempt was made to separate the caecal from the woody droppings. Subsamples were dried at 100° to determine the moisture content.

The birds were fed a pelleted diet (Grouse Breeders pellets, Rank, Hovis, MacDougall Agriculture (Caledonia) Ltd., Riverside Drive, Aberdeen AB9 8DN) with a supplementary bundle of heather twice weekly. Intake of pellets and heather were each determined separately by subtracting the dry weight of the remains from the dry weight of the amount provided (Moss et al. 1972). Samples of pellets, heather and droppings were analyzed for magnesium, nitrogen, phosphorus, calcium, potassium and sodium (Table 1) as in Moss and Parkinson (1972). Eggs were dry ashed and then analyzed by the same methods.

MEASUREMENTS ON WILD BIRDS

Four pairs were studied, at Kerloch moor in Kincardineshire, two in spring 1972 and two in 1973. They were marked with colored plastic back tabs (Blank and Ash 1956). Red Grouse usually form monogamous pairs and occupy exclusive territories (Watson and Jenkins 1968). During the spring, cock and hen accompany each other closely, usually feeding within 2–3 m of each other and roosting within a few meters. They feed sporadically throughout the day, but an hour or two before dusk they begin to feed steadily as they fill their crops for the night (Savory 1974). As spring approaches they tend to concentrate their feeding in one or two favorite spots within the territory (Lance 1975). Of the four pairs watched, one pair could usually be found feeding in one particular spot and the other three pairs were usually seen in one of two different places.

The birds were watched feeding in the evening until they went to roost, choosing different places each night. The observer returned before dawn each morning, watched the birds leave their roosting places and collected their droppings. On top of, or close by, the heap of woody droppings were a few freshly produced caecal droppings. The two kinds of droppings were collected and analyzed separately. The quantity of caecal droppings collected was small and so 2–4 collections of caecal droppings from the same bird were combined to give a weight sufficient for chemical analysis. The cock usually arose a few minutes before the hen and the observer was sometimes unable to find his caecal droppings.

Handfuls of heather were taken from the area where the birds had fed the previous evening. If the cock and hen had fed separately at different spots, separate samples were taken there. If they had moved from one area to another in the course of the evening, samples were taken from both areas. Usually, cock and hen fed over the same, single piece of ground in any one evening, generally no more than a few square meters. In the laboratory, the previous summer's growth of the heather, plus the minute proportion of newly-growing material at the tips, was separated for analysis. (The relationship between samples of this kind and the heather that grouse eat is described below.) Elemental analyses were done separately on each sample of heather and droppings. Three mean values were calculated for each bird, for the food and the two kinds of droppings, and these means used in subsequent calculations. In addition, analyses for energy and proximate constituents (Moss and Parkinson 1972) were made on combined samples. For this, equal weights of each sample were taken so that there was one combined sample each of food, woody and caecal droppings for each bird. Energy was measured in both years but proximate constituents only in 1973.

CALCULATION OF BALANCES AND RETENTION RATIOS

The balance of each dietary component was the amount eaten minus the amount excreted in the droppings (feces and urine). The retention ratio was the balance divided by the amount eaten. For dietary components that are not excreted in the urine to any appreciable extent, e.g. lignin, these ratios are virtually the same as digestibility ratios. Metabolizable energy was the gross energy eaten minus that excreted, divided by the dry weight of food eaten.

TABLE 1. Mean daily DM intake and nutrient balances (mg/d) of four laying hen Red Grouse in captivity, 3 April–20 May 1972.

	DM								
Week	Intake g/d	Retention ratio	Retention g/d	Mg	N	P	Ca	K	Na
1	44	0.48	21	15	230	36	68	70	7
2[a]	45	0.53	24	22	400	86	200	110	16
3[a]	48	0.45	21	16	460	81	220	140	15
4	52	0.49	25	15	430	59	99	80	13
5	55	0.48	26	11	420	22	200	110	16
6[b]	60	0.48	29	22	510	52	310	120	22
7[b]	56	0.52	29	23	480	60	320	110	26
Overall mean	51	0.49	25	18	419	57	201	105	16
Tukey's D[c]	9.3	4.2	4.5	12	158	33	164	65	9
Significance level of differences among weeks:[d]	0.005	0.005	0.005	0.05	0.005	0.005	0.005	0.1	0.005
birds:	0.01	NS	0.01	NS	0.05	NS	NS	0.05	NS

[a] Peak body molt.
[b] Laying. One bird laid her first egg on 30 April (day 5 of week 4), the others on 4 or 5 May (days 4 and 5 of week 5).
[c] Tukey's D is the difference between two values which is significant at the 5% level (J. W. Tukey, quoted by Snedecor (1956)).
[d] From an analysis of variance.

Elemental balances for the captive birds were calculated directly from the measured amount of pellets and heather eaten, the droppings produced and the chemical composition of each.

Savory (1974) measured the food intake of wild hens by counting the number of pecks they made in a day and multiplying this by the mean weight of the particles they had eaten. He calculated that hens ate 97 (SE 10) g/day in April and 100 (SE 13) g/day in early May, before they had started to incubate. For the purposes of this paper I assume that a wild hen eats 100 g dry matter (DM)/day.

For the wild birds, the magnesium (Mg) content of the droppings was used to calculate the retention ratio (A) of dry matter after Moss and Parkinson (1972) and Moss (1973). This is straightforward for birds which are in balance for magnesium:

$$A = 1 - \frac{\text{g/kg Mg in food}}{\text{g/kg Mg in droppings}} \qquad 1)$$

Of the two kinds of droppings produced by grouse, the woody ones form 0.88 of the total and the caecal, 0.12 (Moss and Parkinson 1972). The value for the concentration of Mg in the droppings was therefore a weighted mean:

$$0.88 \times \text{g/kg Mg in woody} + 0.12 \times \text{g/kg Mg in caecal} \qquad 2)$$

The hens, however, were retaining Mg. The value of 18 mg/day determined in captivity (below) was used to correct the Mg content of the wild hens' droppings. To do this it was necessary to know the dry weight of droppings produced each day.

An initial approximation to the weight of droppings was first obtained by calculating the retention of DM with no correction for retained Mg, e.g. for the green-tabbed hen in 1973, this was $1 - 1.55/(2.88 \times 0.88 + 3.29 \times 0.12) = 0.47$ of the food, so that she produced roughly 53 g of droppings each day. A correction of factor $18/53 = 0.34$ g/kg Mg was then added to the original value of 2.93 for the weighted mean of the two kinds of droppings (equation 2) to give 3.27 g/kg Mg. The calculation was then repeated substituting the figure of 3.27 for 2.93 and giving a retention ratio of $1 - 1.55/3.27 = 0.53$, or $100(1 - 0.53) = 47$ g as a second, more accurate approximation to the weight of droppings produced. This led to a second estimate of the correction factor, $18/47 = 0.38$ g/kg, which was now added to 2.93 instead of 0.34, $(2.93 + 0.38 = 3.31)$, and a third estimate of the retention ratio made: $1 - 1.55/3.31 = 0.53$. This value was the same as the second estimate and 0.53 was therefore taken as the retention ratio. In general, the calculations followed this model and were repeated until a constant ratio was reached.

The corrections for Mg retention were quite small. Even if Mg retention by the wild hens was different from that of the captives, this would not alter the results sufficiently to affect the conclusions. For example, under the extreme assumption that wild hens retained twice as much Mg as the captives, this would alter calculated DM retention ratios only by about 0.05.

In principle, it was now possible to calculate retention ratios for the wild hens, except for Mg which was assumed to be the same as in captivity. However, it was not valid to assume that the picked samples of heather were representative of what the birds ate. (Grouse feed selectively and eat heather which differs in chemical composition from that picked by hand.) For spring, the relationships given by Moss (1972b) are

$y = 0.805x + 5.57$ for N
$y = 0.910x + 0.386$ for P
$y = 0.538x + 2.43$ for Ca
$y = 0.436x + 95.7$ for soluble carbohydrate
$y = 0.866x + 7.9$ for crude fat
$y = 0.587x + 33.8$ for soluble tannin

where y is the chemical composition (g/kg) of the crop contents and x that of the picked samples. A sample of 17 birds shot in spring 1970 by C. J. Savory (unpubl. data) showed no significant difference in Mg between hand-picked samples and the crop contents. The only data available for fibrous constituents are from 12 captive birds feeding under semi-natural conditions (Moss 1967a, Moss and Parkinson 1972). There was no consistent difference in α-cellulose or holocellulose but the birds selected against lignin (t for paired variates 4.79, $P < 0.001$) according to

$$y = 1.017x - 27.9 \ (r^2 = 0.48)$$

To calculate retention ratios, the foregoing equations were applied to the observed chemical composition of the picked samples of heather.

For the purposes of calculation, I assumed that the birds ate only heather. In fact, birds on Kerloch eat about 90% heather in spring (Moss 1972b), 8 of the remaining 10% being *Erica tetralix* and *E. cinerea*. The chemical composition of the two *Erica* spp. is usually similar to that of heather. If the Mg content of the *Erica* spp. differed from that of the heather by 0.5 g/kg, a value which is greater than the difference observed by Moss et al. (1972), this would affect the observed retention ratio of DM by less than 0.02.

RESULTS

RETENTION OF ELEMENTS AND DM IN CAPTIVITY

Elemental balances and DM retention were measured in 7 weekly periods from 3 April–22 May 1972. The results are summarized in Table 1. Fuller details may be had from the author on request.

Energy was not measured in the work on captive birds, but the metabolizable energy (ME) of the pellets was 10.9 kJ/g DM (2.6 kcal/g) (unpubl. data) and the ME of heather eaten by captive birds about 5.6 kJ/g (1.3 kcal/g) (Moss and Parkinson 1972). The birds' diet was 9.4% heather (range 8.0–11.4) and so the diet would have had an ME content of about 10.4 kJ/g DM (2.5 kcal/g) and ME intake averaged $10.4 \times 51 = 530$ kJ/d (127 kcal/d).

The Mg balance (18 mg/d) for the hens was assumed to be the same in the wild as in captivity.

RETENTION RATIOS IN WILD HENS

The wild hens started laying about 20 April, two weeks earlier than the captives (Table 1). Droppings and heather (Table 2) were collected from late March until early May: this was again about two calendar weeks in advance of the captives and therefore over similar physiological stages.

The mean retention ratio of heather DM was 0.52 for the wild hens (Table 3). This

TABLE 2. Chemical composition (g/kg DM) and energy content (kJ/g DM) of heather and droppings of wild hen Red Grouse in spring.

	Number of collections	Gross energy	Mg	N	P	Ca	K	Na	Lignin	Holocellulose	α-cellulose	Soluble carbohydrate	Diethyl ether extract	Soluble tannin
Picked heather														
1972 Blue	11	22.0	1.36	11.7	0.84	4.2	5.1	0.64	—	—	—	—	—	—
Pink	17	22.2	1.56	10.5	0.68	5.1	4.5	0.59	—	—	—	—	—	—
1973 Green	15	22.1	1.55	11.6	0.72	4.9	5.0	0.73	270	390	180	190	91	60
Orange	13	22.1	1.44	11.2	0.74	5.0	5.2	0.64	280	390	170	170	87	59
Woody droppings														
Blue	11	22.9	2.52	14.5	0.35	6.5	4.1	0.55	—	—	—	—	—	—
Pink	19	23.0	2.69	13.4	0.32	7.4	4.1	0.65	—	—	—	—	—	—
Green	9	23.2	2.88	15.6	0.21	8.3	2.7	0.75	300	530	240	46	100	66
Orange	8	23.2	2.68	13.6	0.19	7.7	3.2	0.38	230	530	230	44	120	49
Caecal droppings														
Blue	10(3)[a]	21.8	2.03	44.5	9.6	2.6	43	4.0	—	—	—	—	—	—
Pink	19(5)[a]	21.9	3.40	39.2	7.9	2.8	36	3.2	—	—	—	—	—	—
Green	8(3)[a]	21.6	3.29	45.3	7.9	2.3	43	5.1	240	35	20	66	66	190
Orange	7(3)[a]	21.6	2.78	42.5	6.9	2.1	39	5.9	210	25	20	75	66	330

[a] Numbers in parentheses are the number of samples into which these collections were combined for chemical analysis.

TABLE 3. Elemental (mg), DM (g) and energy (kJ) retention by wild hens eating 100 g DM heather/d (retention ratios and ME (kJ/g DM) in parentheses).

	DM	Energy	N	P	Ca	K	Na
Hen							
Blue	52(0.52)	1,110(11.1)	630(0.42)	42(0.37)	180(0.38)	87(0.17)	17(0.27)
Pink	50(0.50)	1,080(10.8)	610(0.44)	39(0.39)	170(0.34)	47(0.11)	11(0.18)
Green	53(0.53)	1,130(11.3)	590(0.40)	51(0.49)	150(0.30)	140(0.29)	14(0.19)
Orange	53(0.53)	1,130(11.3)	660(0.45)	59(0.56)	180(0.35)	160(0.32)	15(0.24)
Means	52.0(0.52)	1,113(11.11)	622(0.43)	48(0.45)	172(0.34)	109(0.22)	14(0.22)
SD	1.4(0.014)	24(0.24)	30(0.022)	9(0.089)	12(0.033)	51(0.099)	3(0.042)

was similar to the captives' diet, as was the ME (11.1 kJ/g). However, food intake of wild hens (100 g/d, Savory 1974) and therefore DM retention and ME intake were all about double the values for captives. The retention ratios for heather were high considering its fibrous nature and were achieved by digesting significant amounts of cellulose and lignin (Table 4).

Balances of P, Ca, Na and K determined for wild birds were similar to those found in captivity. However, wild birds appeared to retain more N (622 mg/d, Table 3) than captives (419 mg/d, Table 1).

Daily DM intake by the captive birds was similar to that for laying chickens (about 400 g/1,000g $W^{0.75}$), compared with 760 g/1,000g $W^{0.75}$ for wild birds.

RETENTION RATIOS IN COCKS

The wild cocks' droppings were analyzed for Mg, energy and proximate constituents. No measurements were made of Mg balance with captive cocks and it was therefore impossible to make the appropriate corrections when calculating retention ratios. But even in the hens, Mg retention was small compared with intake and the corrections correspondingly small. In spring the cocks do not molt until after the hens have laid their eggs, and it is very probable that their Mg balance is closer to zero than that of the hens. It is assumed to be zero.

The cocks ate less heather (63 (SE 6) g/d, Savory 1974) and retained less DM (0.46, Table 5) than the hens (0.52, Table 3). Their daily ME intake was 611 kJ (146 kcal), compared with 1,110 kJ/d (265 kcal) for the hens. ME intake for these cocks was similar to that by Willow Ptarmigan (*Lagopus lagopus*) in winter, both in Arctic Alaska (Moss 1973) and in Arctic USSR (Andreev 1974). Wild cocks ate about the same amount of heather as captive cocks (Table 5), but digested it more efficiently. The captive cocks in this comparison (Table 5) were penned on a natural sward of heather close to where the wild cocks were studied and had no other food provided (Moss and Parkinson 1972). The woody droppings of wild birds (Tables 2 and 6) were similar in chemical composition to those of captives eating heather. However, the wild birds' caecal droppings contained more holocellulose and crude fat and less soluble carbohydrate.

NUTRIENT CONTENT OF EGGS

Laying hens retained nutrients as fast as or faster than they secreted them as eggs, with the exception of Ca (Tables 1, 3 and 7). Presumably, Ca was stored before laying, as in chickens (Common 1938).

DISCUSSION

DIGESTION OF HEATHER BY WILD AND CAPTIVE GROUSE

Wild birds digested heather more efficiently than the captive grouse studied by Moss and Parkinson (1972) (Table 5). This was not unexpected, because captive grouse lose weight on a diet of heather and have much shorter intestines than wild birds (Moss

TABLE 4. Retention ratios for proximate constituents of heather eaten by wild Red Grouse.

Bird	Sex	Lignin	Holo-cellulose	α-cellulose	Soluble carbo-hydrate	Diethyl ether extract	Soluble tannin	DM
Orange	♀	0.59	0.43	0.45	0.88	0.40	0.43	0.53
Green	♀	0.43	0.44	0.41	0.87	0.44	0.45	0.53
Orange	♂	0.45	0.34	0.40	0.89	0.31	0.33	0.46
Green	♂	0.31	0.33	0.29	0.84	0.34	0.24	0.45

TABLE 5. DM and energy balance of four wild and five captive cock Red Grouse eating heather (SE in parentheses).

	Wild	Captive[b]
DM intake (g/d)	63(6)[a]	71(2.9)
DM retention ratio	0.46(0.006)	0.27(0.017)
ME (kJ/g)	9.7(0.05)	5.9(0.36)
ME intake (kJ/d)	611	414(17)

[a] Savory (1974).
[b] Moss and Parkinson (1972).

1972a). The wild birds were also more efficient than captive sheep (Milne 1974) and red deer (*Cervus elaphus*) (Staines 1969) at digesting heather.

A comparison of the composition of droppings from captive (Moss and Parkinson 1972) and wild grouse eating heather (Table 6) showed little difference in woody droppings but marked differences in caecal droppings. Caecal droppings from wild birds contained less soluble carbohydrate, more holocellulose, and much more crude fat than those from captives. This is consistent with the previous suggestion (Moss and Parkinson 1972, 1975) that relatively indigestible materials are concentrated in the caeca while more digestible ones are absorbed. If correct, this implies that the crude fat remaining in the caecal droppings was highly indigestible. Its fourfold increased concentration in the wild birds' caeca compared with the captives', suggests that much more material was absorbed through the wild birds' caeca than the captives'.

Digestibilities *in vivo* and *in vitro* often differ. The difference between wild and captive grouse suggests that the difference between wild and captive animals may be at least as important as the differences between *in vivo* and *in vitro* situations.

ENERGY BALANCES AND FIBRE DIGESTION

Wild hens took in 1,110 kJ ME/d, captives about 530 kJ/d. Wild hens foraged and indulged in other activities not possible in captivity. The energy requirement for these was termed the "cost of free living" by Kendeigh (1970). This can be calculated for cocks by subtracting the daily ME intake found in captivity (380 kJ, Savory 1974) from that in the wild (610 kJ, Table 5) i.e., 230 kJ/d. This is probably a maximum because cocks are active displaying and defending their territories in spring, when they eat more food than in any other season. If we apply this figure to the hens, their energy requirement should have been 530 + 230 = 760, 350 kJ less than actually observed. However, the high intake of food was probably necessary to maintain nutrient balances and the energy available as ME may not have been used efficiently by the birds. Fibre digestion may have provided energy only incidentally, and its main function may have been to make nutrients available by breaking down cell walls.

ELEMENTAL BALANCES AND SELECTION FOR NUTRIENTS BY WILD BIRDS

Wild hens appeared to retain more N (622 mg/d) than captives (419 mg/d). Modafferi (1975) showed that the intestines of wild hen Rock Ptarmigan (*Lagopus mutus*) increase markedly in length and weight in spring; he suggested that they may function as a protein store. A parallel effect may occur in captive Red Grouse (Moss 1972a) but captives must retain less N in their guts than wild birds because captives' intestines are much smaller.

Grouse in spring select heather which contains higher concentrations of N and P than that which is generally available (Moss 1972b). If the hens in the present study had not been selective and had eaten heather of the same chemical composition as the picked samples (11.3 g/kg N, 0.75 g/kg P), the retention ratios for N and P would have to have been increased from 0.43 and 0.45 to 0.55 and 0.64 respectively in order to maintain the observed balances. But the birds required N and P for maintenance in addition to the quantities they retained. This is not known for P but for N is 530 mg/1,000 kJ, as calculated

TABLE 6. Composition (proportion of DM) of droppings from two wild cock Red Grouse and five captives (SD in parentheses) eating heather.

	Woody droppings		Caecal droppings	
	Wild	Captive[a]	Wild	Captive[a]
Lignin	0.30(0.04)	0.27(0.01)	0.19(0.02)	0.13 (0.07)
Holocellulose	0.54(0.001)	0.52(0.02)	0.06(0.01)	<0.02
α-cellulose	0.23(0.02)	0.21(0.02)	<0.02	<0.02
Soluble carbohydrate	0.04(0.01)	0.05(0.01)	0.08(0.00)	0.14 (0.01)
Diethyl ether extract	0.11(0.01)	0.10(0.01)	0.06(0.001)	0.015(0.003)

[a] Moss and Parkinson (1972).

TABLE 7. Rate of output of elements by captive grouse in eggs (SD in parentheses).

	Mg	N	P	Ca	K	Na
mg/egg (n = 10)	10(1)	408(93)	56(9)	589(41)	27(7)	19(4)
mg/d	5.5(0.8)	223(34)	30(5)	322(49)	15(2)	10(2)

from the poultry diet in Wilson et al. (1965) i.e., 530 × 760/1,000 = 403 mg/d. This would increase the necessary digestibility of N to 0.91. But the N in heather cannot be entirely protein, so the true digestibility of protein would have had to approach 1.00, which would probably be impossible. It follows that both the selection (Moss 1972b) and the high food intake (Savory 1974) that are observed are probably essential to the laying hen Red Grouse if she is to maintain the observed N balance. The same may also apply to her P balance.

Savory (1974) showed that captive Red Grouse, feeding on a diet of fertilized heather that contained more N and P than control heather, lost weight more slowly than birds eating the control heather. This, and the calculations above, are in accord with the suggestion that N and/or P are the limiting nutrients in heather eaten by grouse (Moss 1967b).

If this is correct, we might expect changes in breeding success on a moor to be related to variations in the N and/or P content of heather shoots there. Indeed, fertilizing a moor with nitrochalk did improve the birds' breeding success (Miller et al. 1970). However, natural variations in the gross N and P content of heather shoots in spring bore no relation to changes in breeding success (Moss et al. 1975). Instead, variations in breeding were correlated with the number of days that the heather had been growing before the hens finished laying, and also with the density (g/m^2) of heather available to them.

These observations may be reconciled by suggesting that the N and P in the newly-grown heather tips are more readily digested than the N and P in the older parts of the shoots. This suggestion has yet to be tested. In addition, an increased density of heather may improve breeding success by making food selection easier. The more heather there is present, the easier the birds may find it to select a diet providing an adequate plane of nutrition.

SUMMARY

Heather, the main food of Red Grouse, is of poor quality by agricultural standards, containing much fibre and little nitrogen (11 g/kg DM) and phosphorus (0.7 g/kg). Wild, laying hen grouse ate twice as much heather and retained twice as much ME (1,110 kJ/d) as captives (530 kJ/d) eating a pelleted diet. Calculations suggest that wild hens do not actually require all the energy they digest, but have to eat large quantities of food in order to attain adequate N (and possibly P) balances. The selection for heather especially rich in N (and P) which is observed is probably also essential for the wild hens to attain the observed N (and possibly P) balances.

Free-living, wild Red Grouse digested the heather they ate much more efficiently than captives eating the same food. Hence wild birds can survive and breed, while captives lose weight, on a diet of heather. Wild birds digested more cellulose and lignin than captives on the same diet.

ACKNOWLEDGMENTS

It is a pleasure to thank D. King for help in field and laboratory, S. E. Allen, J. A. Parkinson and colleagues of I.T.E.'s Chemical Service for doing chemical analyses and J. Davidson and A. Watson for criticizing the manuscript.

LITERATURE CITED

Andreev, A. V. 1974. Adaptations of tetraonid birds to winter conditions. Zoological investigations of Siberia and the Far East. *In* Proc. symp. biol. probl. north 5:108–111. V. L. Kontrimavichoos, F. B. Chernyavski, V. G. Krivoshyeev [eds.] Acad. Sci. U.S.S.R., Far-Eastern Scientific Centre, Vladivostok (in Russian).

Blank, T. H., and J. S. Ash. 1956. Marker for game birds. J. Wildl. Manage. 20:328–330.

Common, R. H. 1938. Observations on the mineral metabolism of pullets. J. Agric. Sci. 28:348–366.

Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.), in north-east Scotland. J. Anim. Ecol. 32:317–375.

Kendeigh, S. C. 1970. Energy requirements for existence in relation to size of bird. Condor 72: 60–65.

Lance, A. 1975. Aspects of individual performance in red grouse. Ph.D. thesis, University of Aberdeen, Scotland.

Miller, G. R., A. Watson, and D. Jenkins. 1970. Responses of red grouse populations to experimental improvement of their food, p. 323–335. *In* A. Watson [ed.], Animal populations in relation to their food resources. Blackwell Scientific Publications, Oxford.

MILNE, J. A. 1974. The effects of season and age of stand on the nutritive value of heather (*Calluna vulgaris*, L. Hull) to sheep. J. Agric. Sci., Camb. 83:281–288.

MODAFFERI, R. D. 1975. Aspects of morphology in female rock ptarmigan (*Lagopus mutus*) during ovarian recrudescence. Ph.D. thesis, University of Alaska.

MOSS, R. 1967a. Aspects of grouse nutrition. Ph.D. thesis, University of Aberdeen, Scotland.

MOSS, R. 1967b. Probable limiting nutrients in the main food of red grouse (*Lagopus lagopus scoticus*), p. 369–379. *In* K. Petrusewicz, [ed.], Secondary productivity of terrestrial ecosystems, Vol. I. Panstwowe Wydawnictwo Naukowe, Warszawa and Krakow.

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

MOSS, R. 1972b. Food selection by red grouse (*Lagopus lagopus scoticus* (Lath.)) in relation to chemical composition. J. Anim. Ecol. 41:411–428.

MOSS, R. 1973. The digestion and intake of winter foods by wild ptarmigan in Alaska. Condor 75: 293–300.

MOSS, R., G. R. MILLER, AND S. E. ALLEN. 1972. Selection of heather by captive red grouse in relation to the age of the plant. J. Appl. Ecol. 9:771–781.

MOSS, R., AND J. A. PARKINSON. 1972. The digestion of heather (*Calluna vulgaris*) by red grouse (*Lagopus lagopus scoticus*). Br. J. Nutr. 27: 285–298.

MOSS, R., AND J. A. PARKINSON. 1975. The digestion of bulbils (*Polygonum viviparum* L.) and berries (*Vaccinium myrtillus* L. and *Empetrum* sp.) by captive ptarmigan (*Lagopus mutus*). Br. J. Nutr. 33:197–206.

MOSS, R., A. WATSON, AND R. PARR. 1975. A role of nutrition in the population dynamics of some game birds (*Tetraonidae*). Trans. Congr. Int. Un. Game Biol. 11:193–201.

SAVORY, C. J. 1974. The feeding ecology of red grouse in N.E. Scotland. Ph.D. thesis, University of Aberdeen, Scotland.

SNEDECOR, G. W. 1956. Statistical Methods. Fifth ed. Iowa State College Press, Ames, Iowa.

STAINES, B. W. 1969. Digestion of heather by red deer. Proc. Nutr. Soc. 28:21A.

WATSON, A., AND D. JENKINS. 1968. Experiments on population control by territorial behaviour in red grouse. J. Anim. Ecol. 37:595–614.

WATSON, A., AND R. MOSS. 1972. A current model of population dynamics in Red Grouse. Proc. Int. Ornithol. Congr. 15:134–149.

WILSON, H. R., P. W. WALDROUP, J. E. JONES, D. J. DUERRE, AND R. H. HARMS. 1965. Protein levels in growing diets and reproductive performance of cockerels. J. Nutr. 85:29–37.

Institute of Terrestrial Ecology, Blackhall, Banchory, Kincardineshire AB3 3PS, Scotland. Accepted for publication 11 March 1977.