DIGESTION OF DRY MATTER AND ABSORPTION OF WATER IN THE INTESTINE AND CECUM OF ROCK PTARMIGAN

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Despite the many investigations of functional aspects of the hindgut in avian species (Sturkie 1965, Hill 1971, Hudson et al. 1971, Jayne-Williams and Fuller 1971, Ziswiler and Farner 1972), information about digestive function is still incomplete. The primary functions of the hindgut appear to be microbial digestion of carbohydrate and protein, absorption of end products of fermentation, water, some minerals, and microbial synthesis of vitamins. The cecum of all vertebrate herbivores is the main organ of fermentation of the hindgut and in birds attains its greatest size in grouse and ptarmigan. The avian cecum is analogous to ceca of herbivorous mammals and has some functional similarities to the rumen. Well developed ceca enhance the digestion efficiency of plant forage, including plant fiber in the fowl (Radeff 1928, Henning 1929, Suomalainen and Arhimo 1945, Halnan 1949, Thornburn and Wilcox 1965a, 1965b) and cellulose in the Red Grouse (*Lagopus lagopus scoticus*; Moss and Parkinson 1972), in the Ruffed Grouse (*Bonasa umbellus*), Chukar (*Alectoris chukar*), and Bobwhite (*Colinus virginianus*; Inman 1973, Inman and Ringer 1973) and in Rock Ptarmigan (*Lagopus mutus*; Gasaway 1976). Disappearance of dry matter (DM) from the ceca of Ruffed Grouse, Chukar and Bobwhite was estimated and compared to absorption from the intestine (Inman 1973). Bacterial digestion and fermentation of carbohydrates and proteins in the cecum yield volatile fatty acids in domestic fowl (Annison et al. 1968), in ptarmigan (McBee and West 1969, Gasaway 1975a, 1975b) and in Red Grouse (Moss and Parkinson 1972). The transfer of fermentation products and glucose, *in vitro* and *in vivo*, through the wall of the cecum in domestic fowl was reported by Parhon and Barza (1967). Since carbon-14 labeled cellulose fed to ptarmigan was recovered in exhaled CO_2, clearly energy was derived from dietary cellulose (Gasaway 1976).

Other functions, including the absorption of water and electrolytes may also occur in the large intestine and cloaca of the fowl (Schmidt-Neilsen et al. 1963, Nechay and Lutherer 1968, Skadhauge 1967, 1968) and possibly from the cecum (Parhon and Barza 1967, Ziswiler and Farner 1972).

In order to gain insight into the function of the cecum in wild Rock Ptarmigan, we determined routes of flow through the hindgut for water, water-soluble materials and particulate digesta, and estimated the disappearance of DM and water.

MATERIALS AND METHODS

The four Rock Ptarmigan used in the ^{51}Cr-EDTA and Ce-144 trials were 1.5 year old birds raised from chicks captured in the summer of 1970 at Eagle Summit, Alaska (65°30′ N, 145°25′ W). The birds were maintained indoors at 18°C and a daily photoperiod of 18 hr (darkness between 2300 and 0500 hr). Five days prior to the experiment the birds were placed in individual cages. Purina flight conditioner and water were given *ad libitum.*

Three wild adult Rock Ptarmigan were shot April, 1972, at Eagle Summit, Alaska for determination of absorption of the water in the large intestine.

Labeled (^{51}Cr-EDTA and Ce-144) food was substituted for unlabeled food 24 hr prior to the experimental period in order to allow for the equilibration of the marker in the gut. Excreta were collected on wax paper at several hour intervals for the 3-day experimental period and separated into cecal and intestinal droppings. Samples were dried at 80°C for 24 hr in plastic vials and weighed to determine excreta output. Samples were radioassayed and marker concentration calculated.

We determined food consumption daily for 3 consecutive days by measuring weight loss from tared food trays and correcting for spillage.

Loss of water via excreta was estimated by drying periodically collected fresh droppings at 80°C for 24 hr.

The amount of water and DM entering the cecum, expressed as a fraction of water and DM entering the hindgut, was calculated from the respective recoveries of ^{51}Cr-EDTA and Ce-144 in cecal droppings compared with total droppings.

We determined the digestibility of the diet, over a 3-day period, by the total collection method (Kleiber 1961):

$$\%\ \text{Digestibility} = [1 - \frac{(\text{Total excreta g})}{(\text{Total food consumed})}] \times 100 \quad \text{(eq. 1)}$$

Digestibility of the uniformly labeled food and food entering the cecum was determined using the ratio method (Sibbald et al. 1960, Duke et al. 1968):

TABLE 1. Food consumption, digestibility data and the proportion of liquid (^{51}Cr-EDTA) and dry matter (Ce-144) markers recovered in cecal excreta compared with total marker recovered are presented for Rock Ptarmigan fed a diet uniformly labeled with ^{51}Cr-EDTA and Ce-144.

	Bird identification				
	1	2	3	4	Mean
Live weight (g)	453	435	422	384	424 (29)[a]
Food consumption (gDM/day)	28.4	27.7	25.3	26.0	26.9 (1.4)
Excreta output (gDM/day)					
Intestinal	10.0	10.3	8.8	8.7	9.6 (0.8)
Cecal	1.7	1.8	1.8	1.4	1.7 (0.2)
% cecal excreta of total excreted DM	14.5	14.8	17.0	13.9	15.1 (1.4)
Food metabolized (gDM/day)	16.7	15.6	14.7	16.0	15.8 (0.8)
Concentration marker in total excreta (μCi/gDM)/ concentration marker in food (μCi/gDM)					
Ce-144	2.59	2.35	2.50	2.68	2.53 (0.14)
^{51}Cr-EDTA	2.32	2.10	2.40	2.18	2.25 (0.13)
% apparent digestibility of food by method					
Total collection (eq. 1)	58.8	55.4	57.9	61.5	58.3 (2.5)
Ce-144 ratio (eq. 2)	61.5	57.5	60.0	62.6	60.4 (2.2)
^{51}Cr-EDTA ratio (eq. 2)	56.9	52.3	58.3	54.1	55.4 (2.7)
% of total marker recovered in cecal droppings					
Ce-144	20.9	13.1	16.1	20.2	17.6 (3.7)
^{51}Cr-EDTA	87.0	86.1	87.2	85.4	86.4 (0.8)

[a] Mean (standard deviation).

$$\% \text{ Digestibility} = [1 - \frac{(\mu\text{Ci label/g food})}{(\mu\text{Ci label/g excreta})}] \times 100 \qquad \text{(eq. 2)}$$

We calculated the total water excreted in cecal and intestinal feces by applying the ratio of water to DM in excreta samples to the total DM excreted of the respective type of dropping.

Estimates of absorption of the water from the large intestine were made by determining the difference in the proportion of water in proximal and distal large intestinal contents (Grovum and Williams 1973). Contents from the proximal and distal colon were placed in tared glass vials, weighed, and the content of water determined by oven drying. Assuming that no dry matter disappears from the colon, the reduction in g water/g DM between proximal and distal ends of the colon equals the water absorbed. Small amounts of electrolytes were absorbed in the large intestine; however, the error induced was considered insignificant.

We prepared ^{51}Cr-EDTA as described by Downes and McDonald (1964). Cerium was in the form of ^{144}CeCl$_3$. Food was labeled with markers by spraying Purina flight conditioner with an aqueous solution containing approximately 4 μCi Cr-51 and 4 μCi Ce-144 per ml. The labeled food was oven dried and representative samples were taken for radioassay.

Food, cecal and intestinal droppings were radioassayed for Cr-51 and Ce-144 as described by Gasaway et al. (1975).

RESULTS

DIGESTIBILITY OF THE DIET

Food consumption and excreta output averaged 26.9 and 11.3 g DM per day, respectively (table 1). Cecal droppings averaged 15% of the total excreted DM (table 1).

Estimates of digestibility of the food using the total collection method (eq. 1) and the ^{51}Cr-EDTA and Ce-144 ratio methods (eq. 2) were 58.3, 55.4 and 60.4%, respectively (table 1). The estimates of digestibility from the ratio methods were significantly different ($P < 0.05$), but neither differed significantly from the estimates based on the total collection.

Estimates of digestibility over short time intervals using the Ce-144 ratio method followed a daily cyclic pattern in which digestibility reached a peak near 1600 hours and declined throughout the night until midmorning (fig. 1). Highest digestibility coincided with periods of highest rates of intestinal excreta output.

DIGESTION IN THE CECUM

The average concentrations of the DM marker (Ce-144) in intestinal (186 μCi/g DM) and cecal (229 μCi/g DM) droppings were determined and used (fig. 2) to estimate a digestibility of 19% for digesta entering the cecum (eq. 2). Considerable variability was associated with the digestibility estimate and sources of error will be discussed.

PATTERNS OF EXCRETION OF THE MARKERS IN INTESTINAL AND CECAL DROPPINGS

Ce-144 concentration in intestinal droppings showed diurnal oscillations and averaged 2.5 times greater than the concentration in food (fig. 2), while the concentration of Ce-144 in cecal excreta averaged 1.2 times greater than

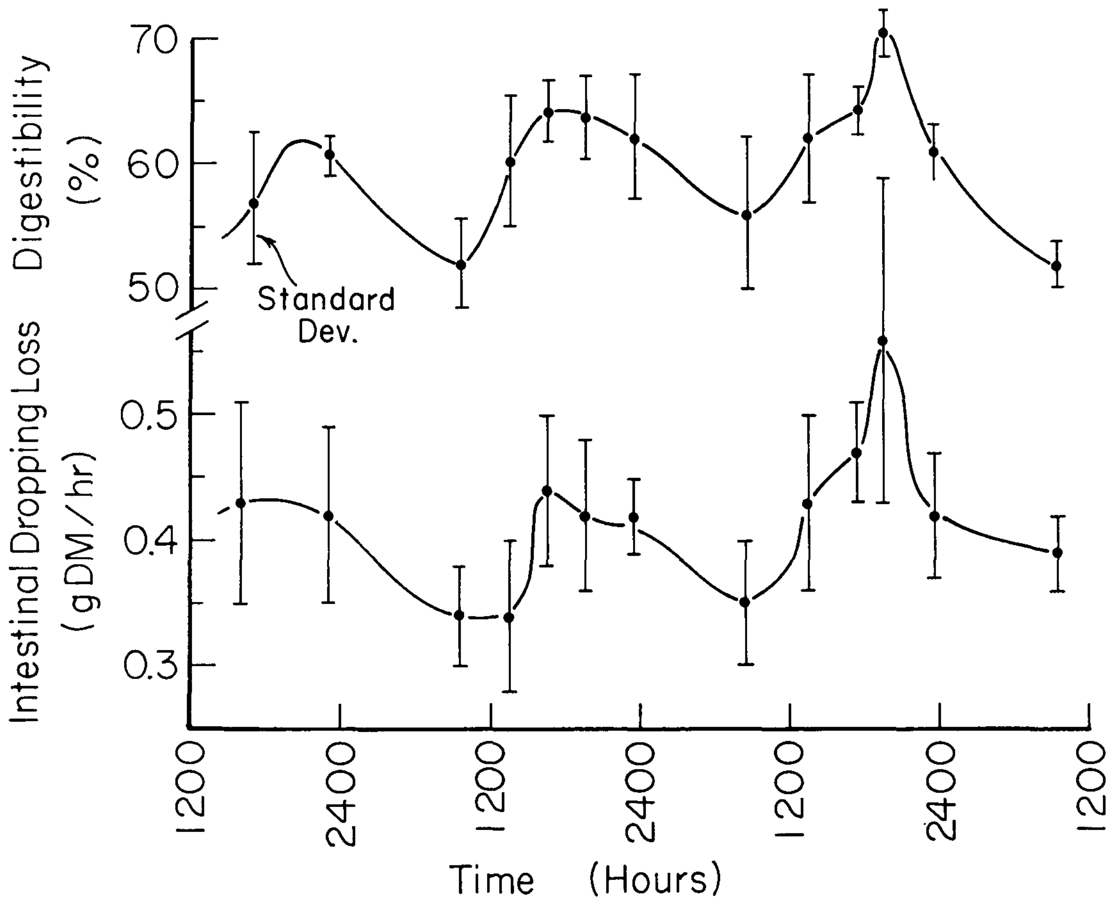

FIGURE 1. Mean rate of fecal DM output and DM digestibility as determined by the nondigestible marker Ce-144.

intestinal excreta and showed no diurnal pattern (fig. 2). Ce-144 concentration of cecal droppings for ptarmigan numbers 2 and 3 were consistently lower than for birds 1 and 4 and in some instances were lower than intestinal droppings for the same period. Cecal droppings contained an average of 17.6% of the DM marker, Ce-144, excreted in total droppings (table 1). The two birds with lowest Ce-144 concentration in cecal excreta also shunted the lowest fraction of the DM (Ce-144) into the cecum (table 1).

Mean ^{51}Cr-EDTA concentration in DM of intestinal droppings was only 0.33 times the concentration in the food (fig. 2), while the concentration of ^{51}Cr-EDTA in cecal droppings was 39 times that of intestinal droppings (fig. 2). Unlike the excretion pattern of Ce-144 no diurnal excretion pattern of ^{51}Cr-EDTA was observed in intestinal droppings. ^{51}Cr-EDTA was primarily diverted to the cecum with soluble components of digesta; 86.4% of recovered ^{51}Cr-EDTA was accounted for in cecal droppings (table 1). This diversion to the cecum accounted for the low ^{51}Cr-EDTA concentration in intestinal droppings. Thus, ^{51}Cr-EDTA could not be used to estimate the digestion of DM; it is strictly a marker of liquid rather than of DM.

ABSORPTION AND LOSS OF WATER FROM THE HINDGUT AND THE PATTERN OF ^{51}Cr-EDTA EXCRETION IN WATER OF EXCRETA

The loss of water in intestinal and cecal droppings of captive ptarmigan was estimated at 23.3 and 5.9 ml/day, respectively (table 2). The ^{51}Cr-EDTA concentration in water from intestinal droppings was relatively uniform during the three-day collection period (fig. 2). However, mean ^{51}Cr-EDTA concentration in water from cecal droppings was 25.5 times higher than in intestinal droppings (table 2), reflecting the large fractions of water absorbed from the cecum compared with the large intestine.

Water absorbed from contents of the large intestine of 3 wild Rock Ptarmigan was estimated to be 12% (SD = 4) of the water entering the large intestine.

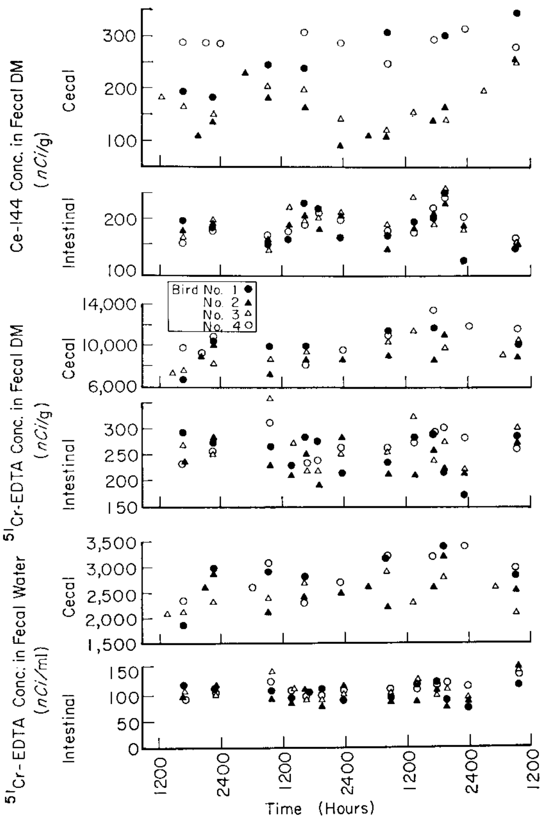

FIGURE 2. The concentration of markers in dry matter and water of cecal and intestinal droppings from 4 Rock Ptarmigan fed a diet labeled with Ce-144 and ^{51}Cr-EDTA.

DISCUSSION

Digestibility estimates of the Purina flight conditioner using ^{51}Cr-EDTA and Ce-144 as nondigestible markers gave good approximation of the total collection method (i.e. 3% under and 2% over, respectively) indicating that both markers were suitable for digestibility studies in ptarmigan. This result is in contrast to findings by Duke et al. (1968) and Inman et al. (1969) who used ^{51}CrCl$_3$ as a marker in Ring-necked Pheasants (*Phasianus colchicus*). In this latter method the digestibility was underestimated by 5–7% compared with the total collection technique.

Since 86% of the ^{51}Cr-EDTA is excreted in only 2 to 4 cecal droppings (i.e. in only 15% of the excreta) per day, it is important to use a sufficiently long sample period to insure a representative sampling of each feces type, otherwise significant errors in digestibility estimates will result. On the other hand, Ce-144 concentration is only slightly higher in cecal than intestinal droppings and hence an incomplete daily recovery of one feces type should have less bias on the final estimate of digestibility. The present diurnal patterns of Ce-144 excretion in ptarmigan are similar to previous findings by Duke et al. (1968) for the excretion of the soluble marker ^{51}CrCl$_3$.

TABLE 2. Fecal water loss and ^{51}Cr-EDTA concentration in water excreted by Rock Ptarmigan fed a diet uniformly marked with ^{51}Cr-EDTA.

Bird no.	Average water excretion (ml/day) Cecal dropping	Intestinal dropping	Relative ^{51}Cr-EDTA concentration per ml fecal water Cecal:intestinal
1	6.0	24.7	27.1:1
2	6.3	25.4	26.1:1
3	6.4	21.7	23.0:1
4	5.0	21.4	25.3:1
	5.9(0.6)[a]	23.3(2.0)	25.5:1

[a] Mean (standard deviation).

A model of daily flow of food, sites of digestion and absorption of DM was constructed (fig. 3). The model is based on feces collections; intestinal droppings amounted to 9.6 g/day and cecal droppings averaged 1.7 g/day or 15% of the total output (table 1). Digestibility of DM in the cecum averaged 19% as calculated from the concentration of Ce-144 in dry intestinal and cecal droppings. Flow of DM into the cecum was therefore 1.7/(1–0.19) or 2.1 g of which 0.4 g was digested and absorbed. Absorption of DM in the large intestine was assumed to be negligible, therefore flow into this portion of the gut equalled the output of intestinal droppings, 9.6 g DM/day. Urine output was unknown, but probably does not exceed 0.4 g DM/day for a bird the size of a ptarmigan (Sykes 1971) and if neglected would contribute only a small error to the estimate of excreta output. The flow of DM through the ileo-cecal-colic (I-C-C) junction (11.7 g DM/day) equalled the amount entering the cecum (2.1 g/day) plus the intestinal droppings (9.6 g DM/day). Food intake was 26.9 g DM/day, therefore the difference, 26.9–11.7 or 15.2 g DM/day, was absorbed in the upper digestive tract. The cecum appeared to play only a minor role in DM digestion in these hand reared, captive Rock Ptarmigan.

Estimates of the disappearance of DM based on changes in marker concentrations may be in error if the marker does not bind with DM uniformly. Nonuniform labeling of the DM with Ce-144 was suggested by a lower concentration of Ce-144 in cecal droppings compared with intestinal droppings during some collection periods in birds number 2 and 3 (fig. 2). In these instances, entry of

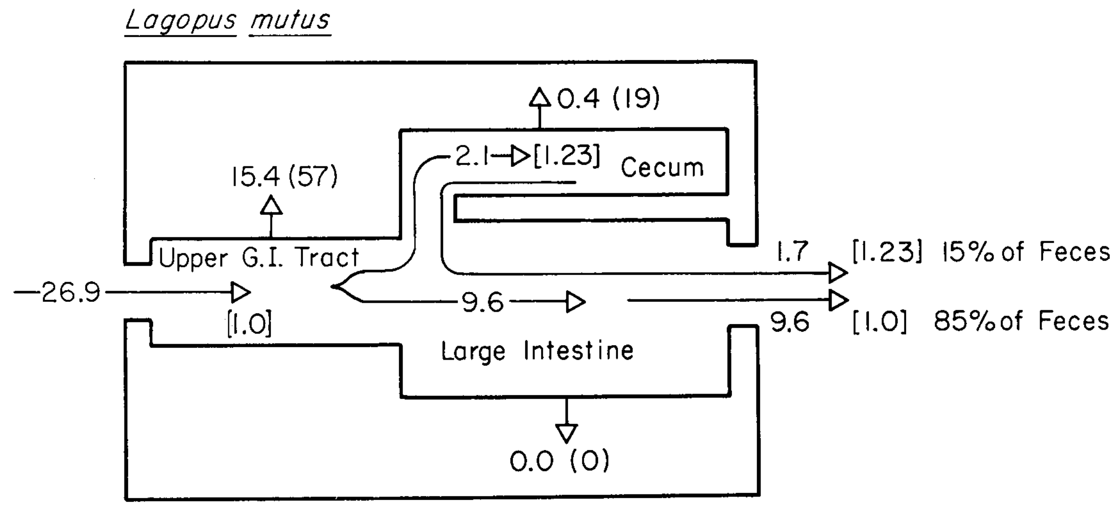

FIGURE 3. Model of daily alimentary dry matter passage and absorption in Rock Ptarmigan. Values are in g/day; ( ), per cent of dry matter entering the digestive organ; [ ], relative concentration of Ce-144 in dry matter.

Ce-144 into the cecum was the lowest and the DM output from the cecum was the highest recorded in the study. We suggest that Ce-144 demonstrated a higher affinity for large rather than small particles and since DM entering the cecum of ptarmigan was composed of very fine particulate matter (Gasaway et al. 1975), spuriously low and variable Ce-144 concentrations were recorded in the cecum. In ptarmigan numbers 1 and 4, the Ce-144 concentration in cecal droppings was greater than that of the intestinal droppings and cecal digestibility was estimated at 33%. Hence, the digestibility estimate of 19% in the cecum and 18% entry into the cecum for DM reaching the hindgut may be minimum values and the digestive role of the cecum may be significantly greater than the present data suggest.

This study showed that caution must be used in interpreting cecal digestibility information obtained from water soluble markers. The concentration of ^{51}Cr-EDTA in cecal DM has little relationship to the digestion of DM occurring in the cecum. In our study, estimates of the digestibility of DM in the cecum using ^{51}Cr-EDTA would be about 97%, an error that highlights the importance of choosing markers when determining DM digestion in specific organs.

Present evidence for separation of liquids and solids points to a model of operation for the entry of material into the cecum of ptarmigan. We hypothesize that hydrostatic pressure is produced at the I-C-C junction through the contraction of the muscular wall of the large intestine of the distal small intestine. A mechanism for the generation of hydrostatic pressure was proposed by Fenna and Boag (1974) who observed in Japanese Quail (*Coturnix coturnix*) peristaltic and antiperistaltic waves in the small and large intestine, respectively, converging at the I-C-C junction. They concluded that these concentrations forced liquids into the cecum. Further, support for an antiperistaltic pressure generating system in domestic fowl was presented by Yasukowa (1959), who observed contractile waves moving anteriorly in the large intestine and passing into the cecum. From reports of Akester et al. (1967) and Nechay et al. (1968), their radioopaque markers move anteriorly in the large intestine. However, in ptarmigan the specific mechanism of cecal filling has not been identified. By maintaining a small controlled orifice into the cecum and by cecal villi acting as filters (Fenna and Boag 1974), only the fluid can be forced into the cecum. Intermittent remixing of the contents in the I-C-C regions and cleaning of the cecal neck orifice would be necessary to accomplish the high degree of separation seen in the ptarmigan. The cecal filling process is continuous (Gasaway et al. 1975), and it is necessary to invoke a reasonably constant hydrostatic pressure filtering process. If cecal filling results from antiperistaltic waves as proposed by Fenna and Boag (1974), frequent alternation of peristaltic and antiperistaltic waves in the large intestine would be required to accomplish a more or less continuous cecal filling and the generally posterior movement of coarse intestinal contents. The watery sus-

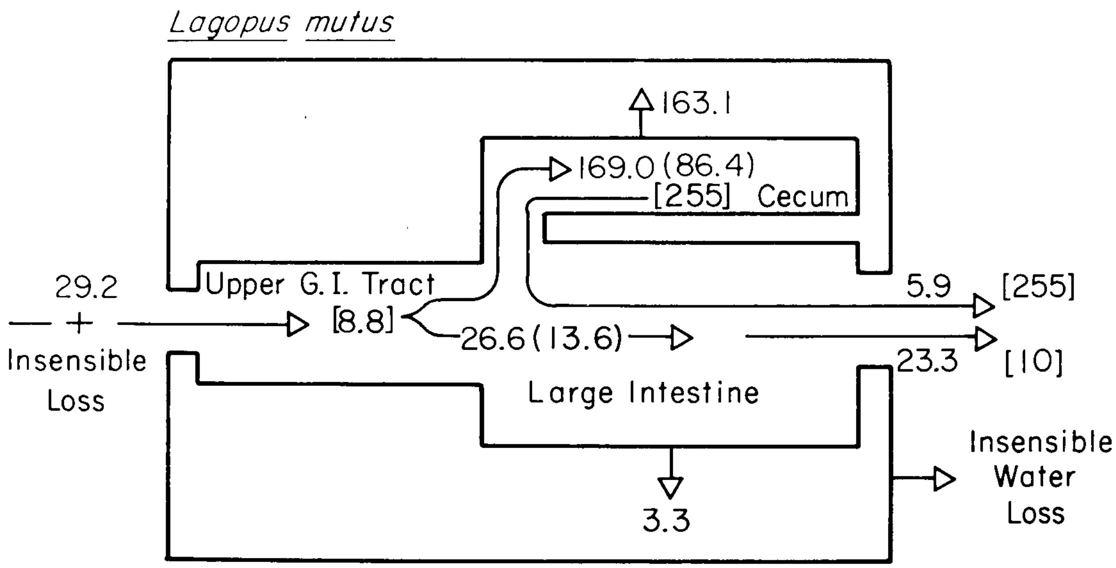

FIGURE 4. Model of daily alimentary water flow and absorption of water from the hindgut of rock ptarmigan. Values are in ml/day; ( ), per cent ^{51}Cr-EDTA entering digestive organ; [ ], relative concentration of ^{51}Cr-EDTA in water.

pension entering the cecum first passes through a 5–8 cm long cecal neck, a thick-walled muscular tube with a small bore relative to the cecum body. Upon entering the cecum it is suggested that contents are moved distally, possibly by peristalsis (Hill 1971) toward the blind end of the cecum.

Our findings for digestion of cecal DM cannot be directly extrapolated to wild birds. Cecal fill (g) of wild Rock Ptarmigan is between 2 and 3 times greater than in hand-reared captive ptarmigan of the present study (Gasaway 1975a, Gasaway et al. 1975), confirming findings by Moss (1972) for Red Grouse. The smaller ceca of captive Rock Ptarmigan appeared to digest proportionately less material than ceca of wild ptarmigan. Our captive ptarmigan digested in the cecum 2.5% of the total DM digested, whereas the energy available from fermentation in the cecum of wild birds was 7% of the free living energy requirements (Gasaway 1975a) or about three times the energy captive birds derived from the cecum.

A high proportion of the food is digested and absorbed in the small intestine of captive ptarmigan when fed a high quality diet (low fiber), hence, a lower proportion of DM consumed reaches the hindgut than in birds feeding on poor quality diets. Therefore, for birds on a high plane of nutrition it may be expected that there is potentially less DM possessing proper physical and chemical qualities necessary to insure a high probability of being diverted into the cecum. Wild Rock Ptarmigan consuming high quality foods during summer have shortened light-weight ceca like captive birds. However, the cecal fermentation rate was sufficiently high during summer to provide as much ME as was measured during other seasons of the year when the cecum was up to twice as large (Gasaway 1975a). From this we conclude that the reduction in size of the cecum in ptarmigan feeding on high quality foods may be an accommodation to a simple reduction in cecal DM input as well as a possible decrease in food intake and energetic requirements. These findings support the observation by Fenna and Boag (1974) that Japanese Quail vary cecal length directly with food consumption.

In spite of the reduced fill of DM in ceca of captive birds, the cecum retains a high efficiency for the absorption of water. The output of water in cecal droppings is only one-sixth of the total water loss in excreta, yet an estimated 86% of water passing the I-C-C junction is diverted into the cecum. Therefore the cecum of Rock Ptarmigan functions as the major site of water absorption in the hindgut.

A model of water flow and absorption was constructed from data collected in this experiment and is summarized in figure 4. The average loss of water from intestinal droppings was 23.3 ml/day. Assuming an absorption of water from the large intestine of 12% for wild birds during winter, 3.3 ml water would be absorbed of the 26.6 ml of water entering from the small intestine. If 26.6 ml water carried 13.6% of the ^{51}Cr-EDTA into the large intestine, it follows that a similar

^{51}Cr-EDTA concentration would exist in water entering the cecum and that 86.4% of the ^{51}Cr-EDTA which entered the cecum would have been transported by 169 ml water. We assumed that passage of cecal droppings was more rapid than intestinal droppings through the large intestine and that essentially no water was absorbed while in passage. Since daily excretion of water in cecal droppings was 5.9 ml, 163.1 ml of water per day was absorbed and 98% of the absorption of water from the hindgut occurred in the cecum.

The values of flow and absorption in figure 4 may also be calculated using the relative ^{51}Cr-EDTA concentration in excreta water. The ratio of the ^{51}Cr-EDTA concentration in water from intestinal excreta to the ^{51}Cr-EDTA concentration in water from cecal excreta was 10:255. Assuming that 12% of the water was absorbed while passing along the large intestine, the concentration value of ^{51}Cr-EDTA in the distal small intestine would be 8.8 μCi/ml water. If the concentration of ^{51}Cr-EDTA in the cecum is 255 μCi/ml water at the time of emptying and 5.9 ml of water were lost per day, 1505 μCi ^{51}Cr-EDTA would have entered the cecum per day. The concentration of ^{51}Cr-EDTA in water entering the cecum was assumed to be 8.8 μCi/ml, therefore 171 ml of water (1505/8.8) would have entered the cecum. Both methods of calculation provide similar rates of entry and absorption for water in the cecum and indicate that the cecum is the major site for alimentary water recovery in the Rock Ptarmigan.

Generally, one of the major functions of the large intestine is water recovery or conservation (Hill 1971, Ziswiler and Farner 1972), but in Rock Ptarmigan this function may be confined to the cecum. Our data support the observation of Duke et al. (1968) that ^{51}CrCl$_3$ concentration in cecal droppings was about two times greater than that of intestinal droppings from pheasants. Also Inman and Ringer (1973) reported 33% and 19–29% of ^{51}CrCl$_3$ is recovered in cecal droppings from Chukars and Bobwhite, respectively. Apparently, the relative effectiveness and importance of the absorption of water in the cecum of these avian species is less than in Rock Ptarmigan and the large intestine may play an increasing role. These data also imply that the hindgut of pheasant, Bobwhite and Chukars probably does not digest and ferment DM as efficiently as that of the Rock Ptarmigan since a greater proportion of the highly fermentable water soluble and fine suspended DM are diverted into the large intestine where little fermentation occurs (Ziswiler and Farner 1972, Moss 1972, Gasaway, unpubl.).

SUMMARY

The routes of flow of water and dry matter (DM) through the hindgut were determined and the disappearance of DM and water were estimated in captive Rock Ptarmigan using radioisotopic markers ^{51}Cr-EDTA and ^{144}CeCl$_3$.

At the ileo-cecal-colic (I-C-C) junction, soluble and very fine particulate DM was diverted into the cecum while coarse material was passed posteriorly in the large intestine. Approximately 18% of the DM, marked by Ce-144 which entered the hindgut, was directed into the cecum and 15% of the total excreted DM was of cecal origin.

Digestibility of the food using the total collection method and the ^{51}Cr-EDTA and Ce-144 ratio methods were 58.3, 55.4 and 60.4%, respectively. Digestibility of material entering the cecum was estimated to be a minimum of 19% or 2.4% of the total digested DM. Thus the cecum appears to play a minor role in digestion of the DM in captive Rock Ptarmigan fed highly digestible foods.

The cecum of the Rock Ptarmigan functions as the major site of water absorption in the hindgut. Of water entering the hindgut 86% was diverted into the cecum. We estimated that 12% and 96% of the water entering the large intestine and cecum, respectively, was absorbed and that 98% of all water absorption from the hindgut occurred from the cecum.

We hypothesize that liquids and suspended DM continuously entered the cecum under hydrostatic pressure generated by the contraction of the small and large intestine in the I-C-C region. Maintenance of a small controlled orifice into the cecum allowed only the fluid fraction to enter the cecum. Following the pressure filtering process the coarse material was propelled down the large intestine by peristaltic waves.

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