FLOW OF DIGESTA IN THE INTESTINE AND CECUM OF THE ROCK PTARMIGAN

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The role of the cecum in digestion of foodstuffs and production of vitamins is not well known for ptarmigan and grouse species. Presumably the function of the avian cecum is to digest and ferment complex carbohydrate molecules, proteins and other nutrients that escape intestinal absorption. The extent of fermentation in the cecum is a product of forage quality, cecum size and mean residence time of dry matter (DM), therefore mechanisms controlling filling and emptying of the cecum determine the kinetics and degree of digestion. Thus, estimates of cecum size and residence time of food particles are necessary in evaluating the role of the cecum in ptarmigan.

Although many studies have used digesta markers in experimental animals, few have dealt with avian species. Early studies by Browne (1922) showed that soluble dyes, which move with the alimentary liquid component, passed through the gut of the fowl faster than food particles. In the Ring-necked Pheasant (*Phasianus colchicus*), $^{51}CrCl_3$, a soluble marker, passed rapidly through the small intestine and colon with a minimum passage time of 1 to 2 hours, while the portion entering the cecum took an average of 35 hours for total passage (Duke et al. 1968). Studies using a barium paste meal indicated that particulate matter may reach the duodenum of the fowl within minutes of ingestion and may be carried along the intestine by rapid peristaltic movements (Vonk and Postma 1949).

Little information exists on the periodicity of cecal filling/emptying or on the ratio of liquid and particulate matter that enters or bypasses the cecum. Judging from the uniformity in concentration of fermentation products in the cecum of the fowl, Hill (1971) suggested that the cecum probably filled at regular intervals. Röseler (1929) observed that the ratio of cecal to normal droppings in the fowl was 1 to 7 after feeding barley and 1 to 11 after feeding wheat, indicating that the amount of digesta entering the cecum may be dependent on the diet. Factors responsible for provoking cecal discharges are not understood; however, Hill (1971) suggested that these factors may be related to the quantity of dead bacteria and undigested material that accumulates in the ceca during fermentation and that requires periodical removal. Hydrogen ion or electrolyte concentration of cecal contents may also influence cecal contractions (Hill 1971).

Except for the reports of McBee and West (1969) the rate of cecal function in ptarmigan has not been documented. Thus, a study of rates of passage of dry matter and water through the intestine and cecum of Rock Ptarmigan (*Lagopus mutus*) was undertaken to gain insight into the regulation of cecal filling and emptying.

MATERIALS AND METHODS

The eight Rock Ptarmigan used in $^{133}BaSO_4$ trials were raised to one year of age in captivity from eggs collected during 1969 near Eagle Summit, Alaska (65°30'N, 145°25'W). These birds were initially raised indoors but were acclimatized to local conditions preceding the experiments. Five days prior to the experiment, the birds were brought indoors and placed in individual cages. Room temperature was maintained at 18°C with an 18 hr photoperiod. Purina game bird chow and water were given *ad libitum*.

The 3 birds used in the ^{51}Cr-EDTA (ethylenediaminetetraacetic acid) and Ce-144 trials were 1.5 year-old Rock Ptarmigan, raised from chicks captured in 1970 at Eagle Summit, Alaska, and maintained indoors under environmental conditions described above. Purina flight conditioner was fed *ad libitum*.

Seventy wild Rock Ptarmigan were shot in conjunction with other cecum studies during various seasons of the year from September 1970 to April 1972 at Eagle Summit and in the Fairbanks area.

Captive birds were given a single dose of marker with a syringe attached to a ⅛" polyethylene tube. During dosing the tube was inserted into the esophagus near the crop-proventricular region. Birds receiving $BaSO_4$ were dosed with 1 μCi Ba-133 (1 ml

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slurry). Those birds receiving both ^{51}Cr-EDTA and Ce-144 were dosed with 12.5 μCi ^{51}Cr-EDTA and 4 μCi Ce-144 (0.6 ml).

Excreta were collected on wax paper, separated into cecal and intestinal origin, air dried, and stored for radioassay. Excreta were collected at periodic intervals for a duration of 2.5 to 3.5 days following dosing with $^{133}BaSO_4$ and for 57.5 hours following dosing with ^{51}Cr-EDTA and Ce-144.

Wild ptarmigan were shot and observations were made on fill, consistency, texture and viscosity of cecal contents. The colon was opened and observations were made on the texture of the contents and on the presence of cecal material.

Rates of passage of water and DM were determined from accumulative excretion curves for ^{51}Cr-EDTA and Ce-144, respectively. The accumulation of 5, 50 and 95% of the marker were used to compare flow rates through the intestine, cecum and entire gut.

The amount of water and DM entering the cecum, expressed as 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.

The fraction of cecal contents emptied per cecal defecation was calculated by assuming that the cecum was dosed by the marker and subsequently uniformly distributed in cecal contents. However, perfect mixing probably does not occur, hence this is a source of error. The total dose of marker entering the cecum was estimated by summing the marker contained in individual cecal droppings. The percentage of cecal fill expelled in each dropping was calculated as follows:

$$\%\text{ of cecal fill emptied in first dropping} = 100 \times \frac{(\mu\text{Ci marker in first dropping})}{(\text{Sum of } \mu\text{Ci marker excreted in cecal feces})}$$

$$\%\text{ of cecal fill emptied in second or succeeding droppings} = 100 \times \frac{(\mu\text{Ci marker in 2nd or succeeding droppings})}{(\text{Sum of } \mu\text{Ci marker excreted in cecal feces}) - (\mu\text{Ci in 1st or sum of preceding droppings})}$$

Barium-133 hydroxide (New England Nuclear, Inc.) was converted into $^{133}BaCl_2$ by mixing with concentrated HCl and then reacted with concentrated H_2SO_4 to form the insoluble$^{133}BaSO_4$ precipitate. The precipitate was washed with water and suspended in a $BaSO_4$ slurry (1 μCi ^{133}Ba/ml).

Preparation of ^{51}Cr-EDTA was as described by Downes and McDonald (1964). Cerium was in the form of $^{144}CeCl_3$. A solution of 20.1 μCi ^{51}Cr-EDTA and 6.7 μCi Ce-144 per ml water was prepared for dosing birds (Ellis and Huston 1968).

Cecal intestinal droppings were radioassayed for Ba-133, ^{51}Cr-EDTA and Ce-144 using a RIDL pulse height analyzer (Nuclear Chicago) coupled to a NaI(TL) detection system. Gamma-ray spectrum stripping techniques were used for quantitating marker concentrations in multiple isotope experiments.

RESULTS

RATE OF CECAL DEFECATION

The average rate of excreta loss from the cecum was 0.042 g DM/hr and the average dropping weighed 0.36 g DM (table 1). Mean time between successive cecal defecations was 8.6 hr. Cecal defecations averaged 2.8 droppings/day and ranged from 2 to 4 droppings/day.

PATTERN OF ^{51}Cr-EDTA AND Ce-144 EXCRETION

Only two birds were used for analysis of the patterns of marker passage and rates of excretion because bird number 1 became very excited at the time of dosing and rapidly passed a large portion of the ^{51}Cr-EDTA in intestinal (non-cecal) droppings. Only 52% of the ^{51}Cr-EDTA entered the cecum of this bird, in contrast to an entree of 95 and 97% of ^{51}Cr-EDTA into the cecum of birds 2 and 3, respectively (table 1). Thus for birds 2 and 3 only 4% of the total ^{51}Cr-EDTA was recovered in intestinal droppings, whereas 87% of Ce-144 was recovered in intestinal dropping (table 1).

Both markers were excreted uniformly in the intestinal droppings, whereas a stepwise pattern of marker excretion was noted in the total (cecal plus intestinal) droppings (fig. 1). The stepwise pattern of excretion of ^{51}Cr-EDTA in total droppings reflects the periodic cecal defecations, whereas the pattern of Ce-144 excretion in total droppings reflects the pattern found in intestinal excreta, since cecal excretion of ^{51}Cr-EDTA represents only 13% of the pathway.

The time required for 5% accumulative excretion through a particular flow route was used as index of transit time (TT). Transit time has been defined as the time from dosing to first appearance of the marker in feces (Grovum and Phillips 1973). The TT of ^{51}Cr-EDTA in intestinal droppings (0.9 hr) was less than for Ce-144 (1.4 hr) (table 2). TT of ^{51}Cr-EDTA in total droppings was greater than for intestinal droppings (table 2) reflecting the delay of marker in the cecum.

The time required for 50% accumulative excretion of marker in intestinal droppings was 3.1 hours and 1.9 hours for ^{51}Cr-EDTA and Ce-144, respectively (table 2). This disparity was even more marked in the comparison of times required for 95% accumulative excretion, namely 18 hours for ^{51}Cr-EDTA and 3 hours for Ce-144. Although the TT for ^{51}Cr-EDTA is less than Ce-144 there is an apparent delay of ^{51}Cr-EDTA passage in

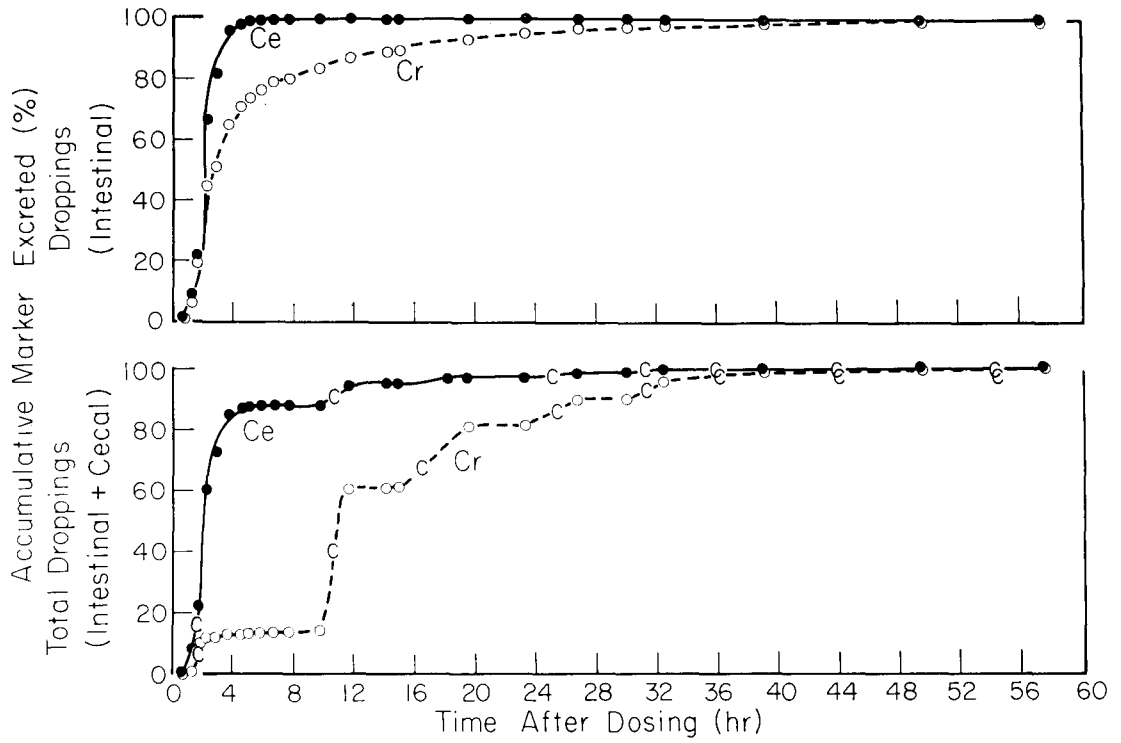

FIGURE 1. The accumulative per cent of markers ^{51}Cr-EDTA and Ce-144 recovered in intestinal and total excreta of Rock Ptarmigan number 2 are shown. Cecal defecation during a collection period is indicated by a "C" on the total excreta curves.

the intestine; this may be due to absorption of ^{51}Cr-EDTA from the cecum followed by reentry in urine. The time required for 95% accumulative excretion of ^{51}Cr-EDTA in total droppings was approximately 26 hours (table 2); this mainly reflected the slow turnover of cecal contents since 96% of the ^{51}Cr-EDTA entered the cecum. In total droppings Ce-144 passed through the gut in considerably less time than ^{51}Cr-EDTA since it was less dependent than ^{51}Cr-EDTA on cecal discharges for its excretion.

DYNAMICS OF CECAL EMPTYING

The proportion of total contents eliminated with each cecal defecation was determined using 3 radioisotopic markers. The percentage of cecal contents voided during each cecal defecation averaged 55% in eight ptarmigan dosed with $^{133}BaSO_4$ (table 3). Mean per cent Ce-144 and ^{51}Cr-EDTA emptied per dropping was 54 and 59, respectively (table 4); a consistent pattern of ^{51}Cr-EDTA emptying at a greater rate than Ce-144 was found. Mean

TABLE 1. The weight and frequency of cecal droppings and the proportion of liquid (^{51}Cr-EDTA) and dry matter (Ce-144) markers recovered in cecal excreta compared with total recovered marker in 3 Rock Ptarmigan.

	Bird identification			
	1	2	3	mean
Weight of average cecal dropping (g dry matter)	0.41(0.15)[a]	0.29(0.13)	0.41(0.06)	0.36(0.13)
Average cecal defecations/day	2.5	3.3	2.5	2.8
% ^{51}Cr-EDTA recovered in cecal excreta	52	95	97	81
% Ce-144 recovered in cecal excreta	13	15	10	13

[a] Mean (standard deviation).

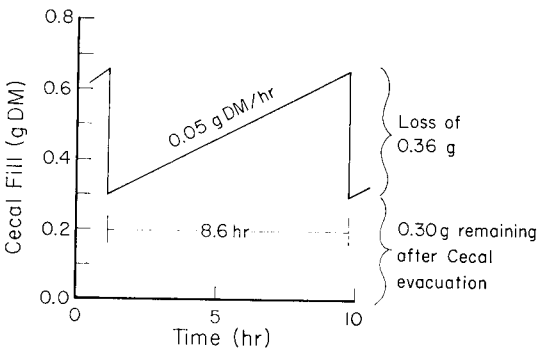

FIGURE 2. Mean cecum filling and emptying cycle in 3 Rock Ptarmigan. The fill rate was calculated from the DM excretion rate adjusted for digestibility (19%, see text) of cecal contents.

rates of emptying estimated from ^{51}Cr-EDTA and Ce-144 differed by 3% in birds number 2 and 3, while in bird number 1 estimates were 8% apart. Estimates of the fraction of cecal contents emptied may differ as much as 15% for an individual dropping using simultaneous ^{51}Cr-EDTA and Ce-144 markers, but generally they were within 6%.

Weights of cecal contents at the time of emptying were estimated from the fraction emptied and the weight of the dropping (table 4). Current evidence suggests that the cecum was not filled to a constant weight before emptying. Maximum cecal fill averaged 0.66 g DM at the time of emptying for a total of 14 fill cycles (table 4). The average cecal fill following a defecation (minimum cecal fill) equalled 0.30 g DM and was calculated as average maximum fill minus average cecal droppings.

Figure 2 summarizes the mean filling and emtpying cycle of Rock Ptarmigan in the present study. The rate of cecum fill was calculated as the rate of cecal feces output plus that fraction of food digested in the cecum. A minimum digestibility of food material in the cecum of Rock Ptarmigan has been estimated at 19% (Gasaway et al., in press).

TABLE 2. Mean time required to eliminate an oral dose of marker via intestinal droppings and total droppings from 2 Rock Ptarmigan. Values were estimated from cumulative excretion curves (fig. 1).

Marker excreted %	Time (hr)			
	Intestinal droppings		Total droppings	
	^{51}Cr-EDTA	Ce-144	^{51}Cr-EDTA	Ce-144
5	0.9	1.4	4.8	1.3
25	1.6	1.7	9.1	1.6
50	3.1	1.9	9.9	1.9
75	5.1	2.2	13.6	2.5
95	18.0	3.0	25.9	10.3

Therefore the fill rate of the cecum was 0.042×1.19 or 0.05 g DM/hr.

TURNOVER OF CECAL CONTENTS

A comparison of curves of concentration versus time for ^{51}Cr-EDTA and Ce-144 in cecal droppings is shown in figure 3. The biological half time ($t_{½}$) or the time required for the concentration (μCi/g DM) to decrease by one-half, was invariably less for ^{51}Cr-EDTA than Ce-144, i.e. 5.7 and 6.2 hours, respectively. Since the average time between cecal defecations was 8.6 hours, from these biological half times it can be calculated that 62% of the Ce-144 marker would have left the cecum. During the same time 65% of the ^{51}Cr-EDTA would have passed through the cecum. Thus, an average of 62—65% of the cecal contents would have emptied during an 8.6 hr period. Both estimates are higher than estimated by our equation for the markers Ce-144, Ba-133 and ^{51}Cr-EDTA, respectively.

The $t_{½}$ for Ce-144 and ^{51}Cr-EDTA in the cecum declined linearly as the mean fraction of cecal contents emptied per defecation increased.

DISCUSSION

In the present studies we assumed that ^{51}Cr-EDTA is a water or liquid marker as has been demonstrated in sheep (Downes and McDonald 1964), and since Ce^{3+} binds to

TABLE 3. Mean per cent of cecal contents emptied per cecal defecation in Rock Ptarmigan as determined by $^{133}BaSO_4$ recovery in cecal droppings (equation in text).

	Mean per cent of cecal contents emptied for individual birds							
	1	2	3	4	5	6	7	8
	52(10)[a]	51(19)	54(12)	54(24)	47(8)	55(36)	68(20)	68(23)
	5[b]	4	6	6	5	3	4	3
Mean of means	55(18)							

[a] Mean (standard deviation).
[b] Number of successive droppings used in estimate.

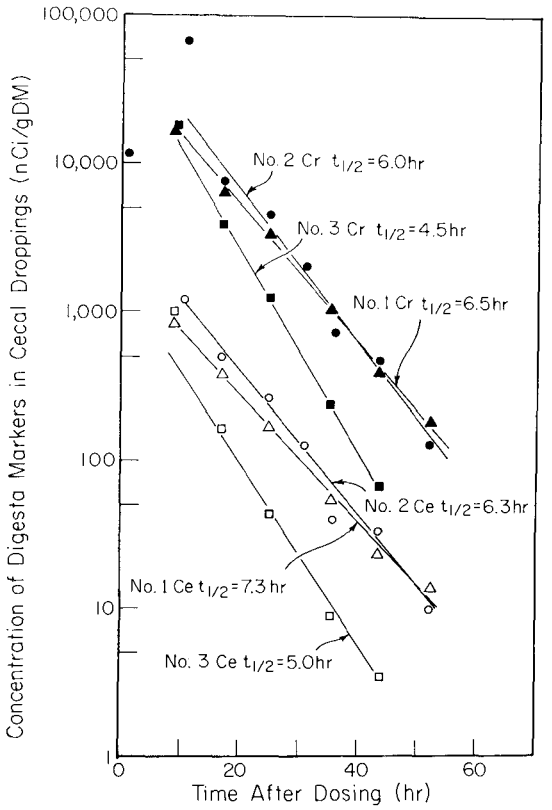

FIGURE 3. The elimination of liquid (^{51}Cr-EDTA) and dry matter (Ce-144) markers from the cecum of Rock Ptarmigan.

organic matter, it was assumed that $^{144}CeCl_3$ behaves as a marker of particulate matter (Ellis and Huston 1968). Thus, the initial excretion of 5% of the separate markers in intestinal and total droppings can be used to deduce the TT of dry matter and liquid phases of digesta through the direct intestinal route and the combined intestinal and cecal routes. Some separation of liquid and solid markers was noted in intestinal droppings since the TT for liquid was less than 1 hour while the TT for particulate matter was approximately 1.4 hr (table 2). Retention of liquid material in the cecum delayed the TT for droppings to almost 5 hr (table 2). The TT, 1–1.5 hr, of the liquid and particulate phases is in good agreement with estimates of 1–3 hr for TT in pheasants using $^{51}CrCl_3$ (Duke et al. 1968). Recent studies by Inman and Ringer (1973) indicate that $^{51}CrCl_3$ behaves more as a liquid marker, whereas in the above mentioned studies of Duke et al. (1968) interpretations were based on the assumption that $^{51}CrCl_3$ was a particle marker.

Care should be practiced in interpreting data using ^{51}Cr-EDTA because Downes and McDonald (1964) have shown that up to 4.7% of ingested ^{51}Cr-EDTA may be absorbed from the alimentary tract of the sheep. Since no ^{51}Cr-EDTA diffuses from the bloodstream to the alimentary tract (Downes and McDonald 1964), all absorbed ^{51}Cr-EDTA is assumed to be excreted in urine, which in birds is added to the intestinal droppings. In the ptarmigan, the most likely site of ^{51}Cr-EDTA absorption would be from the cecum where most of the isotope dose was retained for an extended period of time. Absorption from the cecum, followed by excretion of only 1 to 3% of the total dose of ^{51}Cr-EDTA in urine could account for as much marker as that portion of the dose which moves directly through the intestine and does not enter the cecum. Hence, entry of ^{51}Cr-EDTA from the urine could account for the apparent slow and prolonged recovery of ^{51}Cr-EDTA in intestinal droppings (table 2). In spite of the problems in using ^{51}Cr-EDTA for tracing

TABLE 4. The mean weights of cecal droppings, cecal fill and per cent of cecal contents emptied per cecal defecation for Rock Ptarmigan as determined by ^{51}Cr-EDTA and Ce-144 recovery in cecal droppings (equation in text).

Bird no.	Number of successive cecal droppings	Weight of cecal dropping (g DM)	^{51}Cr-EDTA		Ce-144	
			Cecal fill at time of emptying (g DM)	Contents emptied (%)	Cecal fill at time of emptying (g DM)	Contents emptied (%)
1	5	0.39 (0.15)[a]	0.73 (0.16)	52 (12)	0.91 (0.30)	44 (14)
2	5	0.20 (0.12)	0.54 (0.12)	51 (12)	0.57 (0.13)	48 (12)
3	4	0.42 (0.08)	0.58 (0.08)	73 (8)	0.62 (0.15)	70 (16)
mean of means		0.36 (0.13)	0.66 (0.14)	59 (14)	0.70 (0.25)	54 (17)

[a] Mean (standard deviation).

liquid through the intestines, the first appearance of ^{51}Cr-EDTA in droppings (table 2) may be accurate as an indicator of minimum passage time of water soluble material through the intestine as has been shown for sheep (Grovum and Phillips 1973).

Recovery of ^{51}Cr-EDTA in total droppings occurred more rapidly than the Ce-144, suggesting a differential movement of the dry matter and water soluble material in the gut. For example, ptarmigan number 1, which became very excited when dosed, passed 40% of the ^{51}Cr-EDTA within 1.5 hr, whereas very little Ce-144 was recovered during this period. Apparently the water in which the ^{51}Cr-EDTA was dissolved was not interspersed with other digesta in the gut and passed relatively unmixed through the intestine. This observation confirms the findings of Browne (1922) that the liquid phase of digesta of the fowl passes more rapidly through the gut than particulate matter.

From the low cumulative excretion of Ce-144 in cecal droppings (table 1), we conclude that only a small portion of particulate matter which reaches the ileo-cecal-colic (I-C-C) junction actually enters the cecum in captive Rock Ptarmigan. These data suggest that, provided Ce-144 is uniformly bound to the particulate matter, 10–15% of the particulate matter reaching the I-C-C junction actually enters the cecum (table 1). However, this technique may underestimate dry matter entry into the cecum, for a single dose of Ce-144 passes the I-C-C junction in approximately 3 hours. A more accurate and slightly greater estimate (18%) for entry of cecal dry matter was obtained following continuous dosing of Ce-144 in a separate study on captive Rock Ptarmigan (Gasaway et al., in press). Extrapolation from these data to the field must be done with caution as the fraction of particulate matter entering the ceca of wild Rock Ptarmigan may be greater than that measured in captive Rock Ptarmigan since wild birds have larger ceca and a greater cecal fill (Moss 1972, Gasaway 1975a). On the other hand, total dry matter consumption of wild birds is greater than captive birds, thus necessitating a larger cecum even if there was no change in the fraction of DM entering the cecum. A decreased requirement for cecal function seems possible for captive birds which are fed high quality diets, since a smaller proportion of the highly digestible food will reach the hindgut, and this could account for the apparent decrease in cecal size.

From the high recoveries (95–97%) of ^{51}Cr-EDTA in cecal droppings of undisturbed birds (table 1), we conclude that a large proportion of liquid and suspended material which reaches the I-C-C region is diverted into the cecum. Studies of morphology indicate that the opening into the cecum is small; combined with present observations of low entry of particulate matter into the cecum, we infer that the cecal orifice allows only very fine suspended particles and soluble material to enter. Again, estimates from single dose experiments may be in error due to short term changes in filling rates. However, the errors are apparently small, for in a subsequent experiment (Gasaway et al., in press) we found that 86% of the liquid fraction enters the cecum when ^{51}Cr-EDTA is administered continuously over a 3-day period. A small fraction of $^{51}CrCl_3$ enters the cecum of pheasants (Duke et al. 1968) compared with current estimates of ^{51}Cr-EDTA in the ptarmigan. This difference could be due to a number of factors, the most likely being the relatively larger ceca in Rock Ptarmigan compared with the ceca in the pheasant.

In our model of the cecal filling and emptying process (fig. 2) we hypothesize that cecal filling is continuous between evacuations in Rock Ptarmigan. Evidence supporting this is the following:

(a) Ptarmigan fed ^{51}Cr-EDTA continuously as labeled food demonstrated a relatively constant level of radioactivity per ml H_2O output in the feces (Gasaway et al., in press) and the concentration of ^{51}Cr-EDTA in cecal droppings was very high compared to intestinal droppings. Hence, if cecal contents were leaked to the colon and were recovered in intestinal droppings, or if material that would have entered the cecum was diverted down the colon, a periodic large increase in ^{51}Cr-EDTA concentration would have been observed in intestinal droppings. Therefore, the data suggest that cecal filling is a continuous one-way flow followed by periodic emptying.

(b) We have observed that in wild ptarmigan which had recently emptied their ceca, the proximal two-thirds of the cecum is usually empty, and an appreciable amount of material bearing a close resemblance to cecal droppings is to be found in the distal third. Where contents were noted in the proximal end of the cecum, their texture, color and moisture content more closely resembled those of contents of the distal small intestine, suggesting their recent entry into the cecum.

However, in wild ptarmigan in which the cecum was near maximum fill, the entire cecum was filled with a viscous material characteristic of cecal droppings. Thus the cecum appeared to fill almost continuously with material from the small intestines and the cecal material was then discharged periodically.

Retrograde flow of digesta and urine from the colon into the cecum has been observed in domestic fowl by Akester et al. (1967), Nechay et al. (1968) and Skadhauge (1968) and is the result of antiperistaltic movements. Akester et al. (1967) and Hill (1971) suggested retrograde flow may provide more efficient recovery of electrolytes, water and nutrients and provide a nitrogen source for cecal microbes. Fenna and Boag (1974a) observed antiperistaltic waves in the large intestine which continued into the cecum of Japanese Quail (*Coturnix coturnix*); these waves appeared to transport radioopaque $BaSO_4$ anteriorly in the large intestine and force the liquid phase into the cecum. The extent and significance of retrograde flow in the hind gut of ptarmigan is unknown.

The preferential diversion of the soluble and suspended fractions of digesta to the cecum (table 1, fig. 1) may effect maximal cecal fermentation since very fine particles are more easily degraded by microbial enzymes than large particles due to their larger ratio of surface to volume. The mean time of retention of material entering the cecum and hence the mean time digesta was exposed to bacterial digestion and fermentation was approximately 6 hours (fig. 3). However, a small amount of digesta remains in the cecum for more than 24 hours. The period that particles remained in the cecum varies among individual birds and the retention time decreased as the mean percentage emptied per defecation increased (Gasaway 1974). No correlation was found between the retention time of markers in the cecum and the frequency of defecations.

Selection in browsing birds is directed towards highly efficient and light weight ceca (Fenna and Boag 1974b). The important component in maintaining small ceca which allow for optimum fermentation may involve efficient separation of digesta into soluble and insoluble components and the shunting of highly fermentable substrates into the cecum. Birds have developed more efficient ceca than mammals (Gasaway 1975b) as a result of the selective separation of digesta in the I-C-C region.

Cecal emptying apparently occurs as a rapid, strong peristaltic motion beginning at the distal end of the cecum and passing along the neck and body of the cecum and subsequently down the colon (Hill 1971). Both cecal pouches in Rock Ptarmigan appear to have a similar emptying rate based on the observation that wild birds had nearly equal volumes of contents in both ceca, which suggests that filling and emptying were accomplished in phase. Results of the present study indicated that between 54% and 59% of the total contents were voided per cecal defecation (tables 3 and 4). The contents retained in a cecum following a defecation (fig. 2) presumably provided a ready reservoir of inoculum for new material, thus minimizing the lag time while bacterial numbers increased.

A comparison of minimum and maximum cecal fill in wild Rock Ptarmigan (Gasaway 1975a) was used as an approximation to the proportion of cecal contents evacuated in a single dropping. These measurements indicated that approximately 70% of the contents were discharged in each cecal dropping. This value would be a maximal estimate as the minimum and maximum fills were selected. Hence, the average contents emptied per evacuation cycle may be similar to the present estimate for captive birds.

Cecal fill at the initiation of emptying was highly variable in ptarmigan (Gasaway 1974) suggesting that the level of fill was not the critical factor initiating cecal defecation. Estimates of maximum cecal fill ranged from 0.36 to 1.29 with a mean of 0.66 g DM (fig. 2). If either the available space within a cecum or distention of the cecal wall were controlling the level of fill, and hence the emptying schedule, a reasonably constant fill between successive droppings would be expected. Hill (1971) suggested that cecal distention or hydrogen ion concentration or electrolyte concentration of cecal contents may influence emptying since all these factors affect cecal contractions *in vitro*. Also, the frequency of cecal emptying in chickens is affected by the type of diet (Hill 1971). Captive ptarmigan held outdoors averaged approximately 2 cecal droppings per day when fed Purina game bird chow and seeds (Gasaway, unpublished observations), while ptarmigan raised indoors produced 2.8 (table 1) and 3.2 (Gasaway et al., in press) cecal droppings per day, respectively. Apparently several factors influence the frequency of cecal discharge, and the factors and mechanism responsible for initiating cecal discharge are not understood.

SUMMARY

The flow of liquid and dry matter (DM) digesta through the intestine and cecum of captive Rock Ptarmigan was studied using a single dose of 3 radioisotopic markers, $^{133}BaSO_4$, ^{51}Cr-EDTA and $^{144}CeCl_3$ and from observations on shot wild birds.

A differential rate of liquid (^{51}Cr-EDTA) and dry matter (Ce-144) flow occurred in the intestine. The liquid phase moved faster than dry matter. Liquid digesta entering the ileo-cecal-colic junction was almost entirely diverted into the cecum (96%) whereas only 13% of the DM marker entered the cecum.

The mean particle retention time in the intestine was 2 hours while 95% of the dry matter marker not entering the cecum was excreted in 3 hours. Mean retention time of cecal dry matter was 6–8 hours and 95% of the DM was replaced in 26 hours. The percentage of cecal contents emptied per cecal defecation averaged 56% and time between cecal defecations averaged 8.6 hours. Cecal fill at time of emptying was highly variable, indicating that cecal fill was a minor factor in initiating cecal discharge.

It was hypothesized that the cecum fills continuously between cecal defecations. No evidence for cecal filling from retrograde flow was found for Rock Ptarmigan. Contents retained in the cecum after defecation presumably provide a reservoir of innoculum, thus minimizing the lag time while cecal bacteria numbers increased. Preferential diversion of the soluble and suspended fractions of digesta to the cecum may be responsible for the more efficient and lighter weight ceca of ptarmigan than has been found in mammals.

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