CECAL FUNCTION IN PTARMIGAN

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CECAL FUNCTION IN PTARMIGAN

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ABSTRACT

Cecal functions in wild and captive rock, Lagopus mutus, and willow ptarmigan, Lagopus lagopus, were studied. The flow rates, routes of passage, digestion and absorption of liquid and dry matter (DM) in the intestine and cecum were estimated using radioisotopic markers. Dry matter not entering the cecum passed the length of the gut in 2 hr, whereas particles entering the cecum were retained an additional 6 to 8 hr. An estimated 18% of the DM entering the hindgut was diverted into the cecum where 19% of this DM was digested and absorbed. Cecal filling was continuous between defecations with fluid digesta (liquid and fine suspended particles) and it was hypothesized that the fluid digesta was forced through the small cecal valve by hydrostatic pressure generated from the contraction of the small and large intestines at the ileo-cecal-colic junction. Cecal defecations occurred at approximately 9 hr intervals and voided a mean of 56% of the contents. Eighty-six per cent of the water entering the hindgut from the small intestine was diverted into the cecum and 98% of the water absorption in the hindgut occurred in the cecum.

Foods selected during summer by rock ptarmigan were of higher quality than foods selected during other seasons. The length, weight and content of the cecum were greatest during winter, declined to its smallest size during summer and increased during fall. Total volatile fatty acid (VFA) produced/day in the cecum of the rock ptramigan did not vary significantly among seasons in spite of changing food quality and cecum size. Metabolizable energy (ME) available from VFA averaged

7.1 kcal/day for rock ptarmigan and 5.7 kcal/day for willow ptarmigan. These ME values could supply an estimated 18% and 11% of standard metabolism for rock and willow ptarmigan, respectively.

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INTRODUCTION

Rock ptarmigan, Lagopus mutus, and willow ptarmigan, L. lagopus, are found in the arctic and subarctic of North America and Eurasia. Ptarmigan generally feed on buds, twigs, catkins and berries of woody plants during winter and on leaves, seeds and berries of many plant species during other seasons (Watson, 1964; West & Meng, 1966; Moss, 1968; Weeden, 1969; Gardarsson & Moss, 1970). In ptarmigan and other avian species which have similar herbivorous food habits, the cecum is well developed. The cecum consists of a pair of blind tubular sacs which join the gut at the junction of the small and large intestine. The cecum is a relatively large organ compared to the other portions of the gut ranging from about 80% of the length of the small intestine in rock ptarmigan to 140% in red grouse, Lagopus lagopus scoticus (Modafferi, pers. comm.; Moss, 1972). The cecum "houses" a large microbial population which exists in a commensal relationship with the avian host (Annison et al., 1968; McBee & West, 1969). The microbes digest and metabolize soluble and complex carbohydrate molecules including cellulose which cannot be degraded by avian enzymes. Protein and nonprotein nitrogen are metabolized by the microbes for energy and are synthesized to microbial protein. These substrates, in addition to supplying energy and building material for microbes, are metabolized to products useful to the avian host by microbial fermentation. Volatile fatty acids (VFA) are the major end product of fermentation and their major site of production in the fowl is the cecum (Annison et al., 1968). Fermentation products are a significant source of energy to avian herbivores and provided 11

to 18% of the resting energy requirements and 4 to 7% of free living energy requirements for ptarmigan in the present studies. In addition to the absorption of VFA and possibly amino acids, the cecum is a major site for water and electrolyte recovery in the hindgut (cecum and large intestine). One of the least understood cecal functions is microbial vitamin synthesis and absorption. The presence of abundant B vitamins in the cecum has long been known, however the site of absorption, if they are absorbed, has yet to be defined (Jayne-Williams & Fuller, 1971). In a recent review, McNab (1973) concluded vitamins synthesized in the ceca are unlikely to benefit the host unless coprophagy is practiced. This is an interesting observation since there is no evidence for coprophagy in ptarmigan (G. West, L. Irving, R. Moss, R. Modafferi & R. Weeden, pers. comm.). Thus a ready source of vitamins may be unavailable to ptarmigan.

Considering the large size of the cecum in comparison to the intestine of wild grouse and ptarmigan, the cecum is likely to provide significant survival value from the nutritional standpoint. Metabolizable energy available from cecal digestion may be most important during conditions of restricted food intake or declining food quality. These conditions may exist locally during late winter following heavy browsing by ptarmigan and during winter storms when feeding activity may be restricted. Birds feeding on high quality diets, as during summer, probably have less requirement for the increased digestive efficiency associated with cecal fermentation as long as food quantity is not limited.

Recent reviews on avian nutrition point to the dearth of knowledge on cecal function (Farner, 1960; Sturkie, 1965; Coates & Jayne-Williams,

1966; Hill, 1971a, 1971b; Hudson et al., 1971; Jayne-Williams & Fuller, 1971; Ziswiler & Farner, 1972; McNab, 1973). Therefore, a study of the digestive aspects of cecal function was initiated. Ptarmigan were selected as the experimental bird because of the extensive life history and nutritional background information available and because ptarmigan possess a highly developed cecum. Four facets of the digestive functions of the cecum were investigated, each of which is presented as a chapter in this thesis. First, it was felt that a basic understanding was required of the rate of passage of nutrients through the digestive tract, the time material spent in the cecum, the amount of material entering the cecum and the proportion of cecal content emptied per cecal defecation. Second, the physical nature of material entering the cecum and its mode of entry were investigated. The proportion of food consumed that entered the cecum and the fraction digested were estimated along with water entry and absorption in the large intestine and cecum of captive birds. Third, the quantitative aspects of cecal fermentation in wild rock ptarmigan were investigated during five seasons to determine the relationship between cecum size, forage quality and metabolizable energy (ME) available from microbial VFA production. And fourth, an interspecific comparison of cecal fermentation was conducted with willow ptarmigan.

The chapters of this thesis have been written following the instructions for preparation of manuscripts of The Condor (Chapters I and II) and Comparative Biochemistry and Physiology (Chapters III and IV) where they will be submitted; some duplication will be found in their respective

introductory sections and bibliographies.

REFERENCES

ANNISON E. F., HILL K. J. & KENWORTHY R. (1968) Volatile fatty acids in the digestive tract of the fowl. Br. J. Nutr. 22, 207-216.

COATES M. E. & JAYNE-WILLIAMS D. J. (1966) Current views on the role of the gut flora in nutrition of the chicken. In: Physiology of the Domestic Fowl. (Edited by Horton-Smith C. & Amoroso E.), pp. 181-198, Oliver and Boyd, Edinburgh.

FARNER D. S. (1960) Digestion and the digestive system. In: Biology and Comparative Physiology of Birds. (Edited by Marshall A. J.), pp. 411-467, Vol. I, Academic Press, New York.

GARDARSSON A. & MOSS R. (1970) Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. In: Animal Populations in Relation to Their Food Resources. (Edited by Watson A.), pp. 47-71, Blackwell Scientific Publications, Oxford, England.

HILL K. J. (1971a) The structure of the alimentary tract. In: Physiology and Biochemistry of the Domestic Fowl. (Edited by Bell D. J. & Freeman B. M.), pp. 1-23, Vol. I, Academic Press, New York.

HILL K. J. (1971b) The physiology of digestion. In: Physiology and Biochemistry of the Domestic Fowl. (Edited by Bell D. J. & Freeman B. M.), pp. 25-49, Vol. I., Academic Press, New York.

HUDSON D. A., LEVIN R. J. & SMYTH D. H. (1971) Absorption from the alimentary tract. In: Physiology and Biochemistry of the Domestic Fowl. (Edited by Bell D. J. & Freeman B. M.), pp. 51-71, Vol. I., Academic Press, New York.

JAYNE-WILLIAMS D. J. & FULLER R. (1971) The influence of the intestinal microflora on nutrition. In: Physiology and Biochemistry of the Domestic Fowl. (Edited by Bell D. S. & Freeman B. M.), pp. 73-92, Vol. I, Academic Press, New York.

McBEE R. H. & WEST G. C. (1969) Cecal fermentation in the willow ptarmigan. Condor 71, 54-58.

MOSS R. (1968) Food selection and nutrition in ptarmigan (Lagopus mutus). Symp. Zool. Soc. Lond. 21, 207-216.

MOSS R. (1972) Effects of captivity on gut lengths in red grouse. J. Wildl. Mgmt. 36, 99-104.

McNAB J. (1973) The avian caeca: a review. World's Poult. Sci. J. 29, 251-263.

STURKIE P. D. (1965) Avian Physiology. Cornell University Press, Ithaca, New York, p. 766.

WATSON A. (1964) The food of ptarmigan (Lagopus mutus) in Scotland. Scottish Naturalist 71, 60-66.

WEEDEN R. (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86, 271-281.

WEST G. C. & MENG M. S. (1966) Nutrition of the willow ptarmigan in northern Alaska. Auk 83, 603-615.

ZISWILER V. & FARNER D. S. (1972) Digestion and the digestive system. In: Avian Biology. pp. 343-430, Vol. II, Academic Press, New York.

CHAPTER I.

DIGESTA FLOW IN THE INTESTINE AND CECUM OF THE ROCK PTARMIGAN

INTRODUCTION

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 which escape intestinal absorption. The extent of fermentation in the cecum is a product of forage quality, cecum size and mean residence time, 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 the ptarmigan.

Although there have been many studies using digesta markers in mammals, few have dealt with avian species. Early studies by Browne (1922) showed that soluble dyes, that move with the alimentry 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, however the portion entering the cecum took an average of 35 hours for passage (Duke et al. 1968). The movement of food particles has been studied using insoluble markers which move at the same rate as the food particles (Browne 1922). 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 duodenum and jejunem by rapid peristaltic movements (Vonk and

Postma 1949).

Evidence for the mode of entry of liquid and particulate matter into the cecum is equivocal. For example, Akester et al. (1967) and Nechay et al. (1968) showed that a radiopaque liquid marker moved from the ureter to the colon and entered the cecum of the fowl by retrograde flow, i.e., the movement of material anteriorly in the gut by reverse peristalsis. Hill (1971) suggested retrograde flow functioned as a mechanism for water and electrolyte entry into the cecum where absorption could take place. However Moss (1972) found no evidence for the entry of urine into the cecum, which suggested the absence of retrograde flow to the cecum in red grouse, Lagopus lagopus scoticus. There is little information on the periodicity of cecal filling and emptying and also on the ratio of liquid and particulate matter which enters or bypasses the cecum. Judging from the uniformity in concentration of fermentation products Hill (1971) suggested that the cecum probably filled at regular intervals. The amount of digesta entering the cecum may be dependent on the diet, since Röseler (1929) observed the ratio of cecal to normal droppings in the fowl was 1 to 7 after feeding barley and 1 to 11 after feeding wheat. 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 undigestible material accumulated in the ceca during fermentation, requiring 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 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 preceeding the experiments. Five days prior to the experiment the birds were placed in individual wire mesh (1.3 x 2.5 cm) cages and brought indoors. Room temperature was maintained at 18°C with an 18 hour photoperiod. Purina game bird chow and water were given ad libitum.

The 3 birds used in the ^{51}Cr-EDTA and Ce-144 trials were 1.5 year old rock ptarmigan, raised from chicks captured in the summer of 1970 at Eagle Summit, Alaska. They were maintained indoors at 18°C and a daily photoperiod of 18 hours. Birds were placed in individual cages similar to those described above and were fed Purina flight conditioner 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. Observation

on cecal fill and the type of material entering were made and reported on in the discussion.

Captive birds were given a single dose of marker with a syringe attached to a 1/8" polyethylene tube. During dosing the tube was inserted into the esophagus near the crop-proventricular area. Birds receiving $BaSO_4$ were dosed with 1 μCi Ba-133 (1 ml slurry). Those birds receiving both ^{51}Cr-EDTA and Ce-144 were dosed with 12.5 μCi Cr-51 and 4 μCi Ce-144 (0.6 ml).

Excreta was collected on wax paper, separated into cecal and intestinal origin, air dried, and stored in 14 dram plastic vials for radioassay. Excreta was collected at periodical 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 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.

Passage rates of water and dry matter (DM) were determined from accumulative marker excretion curves for ^{51}Cr-EDTA and Ce-144, respectively. 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 proportions of water and DM entering the hindgut, was calculated from the respective recoveries of Cr-51 and Ce-144 in cecal droppings compared with total droppings.

The proportion of cecal contents emptied per cecal defecation was calculated by assuming that the cecum was dosed by the marker and subsequently uniformly distributed with cecal contents. The total dose of marker entering the cecum was obtained by summing the activities of individual cecal droppings over the 57.5 hour collection period following the initial dosing. The percentage of cecal fill expelled in each dropping was calculated from the amount of marker leaving the cecum in each successive cecal dropping, expressed as a fraction of the marker remaining in the cecum. The formula for calculations were as follows: (eq. 1)

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

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

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 (Ellis and Huston 1968) per ml water was prepared for dosing birds.

Cecal and intestinal droppings were radioassayed for Ba-133, Cr-51

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

Cecal Defecation Rate

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

^{51}Cr-EDTA and Ce-144 Excretion Pattern

Only two birds were used for analysis of marker passage patterns and excretion rates because bird number 1 became very excited at the time of dosing and passed a large portion of the ^{51}Cr-EDTA in intestinal droppings shortly after dosing. 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 Cr-51 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 (non-cecal)

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
% Cr-51 recovered in cecal excreta	52	95	97	81
% Ce-144 recovered in cecal excreta	13	15	10	13

[a]Mean (standard deviation).

droppings whereas a stepwise pattern of marker excretion was noted in the total (cecal plus intestinal) droppings. An example of the pattern of marker excretion is shown in figure 1. The pattern of excretion of ^{51}Cr-EDTA in total feces reflects the stepwise pattern of periodic cecal defecation, whereas the excretion of Ce-144 in total droppings reflects excretion pattern for intestinal feces since cecal excretion of Cr-51 only represents 13% of the pathway.

The time required for 5% accumulative excretion 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$_2$ (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$_2$, 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$_2$. Although the TT for ^{51}Cr-EDTA is less than Ce-144$_2$ there is an apparent delay of ^{51}Cr-EDTA passage in the intestine; this may be due to absorption of Cr-51 from the gut followed by re-entry in urine. The time required for 95% accumulative excretion of ^{51}Cr-EDTA in total droppings was approximately 26 hours (table 2) and mainly reflected the turnover of cecal contents since 96% of the ^{51}Cr-EDTA entered the cecum. Hence 26 hours was required for 3 cecal emptyings,

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.

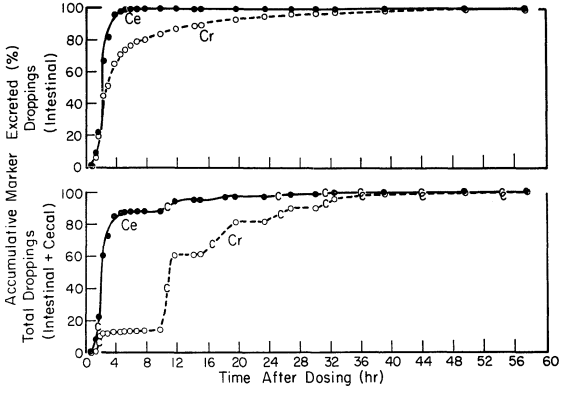


TABLE 2. Mean time required to eliminate an oral dose of marker via intestinal droppings and total droppings from 2 rock ptarmigan. Values were estimated from cumulative excretion curves (fig. 1).

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

assuming a cecal defecation rate was 2.8 per day, and 26 hours would allow for 95% replacement of the marker plus the digesta entering the cecum with the marker. In total droppings Ce-144_2 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 consistant pattern of higher per cent Cr-51 emptied than Ce-144 was shown in all three birds. Mean rates of emptying estimated from Cr-51 and Ce-144 differed by 3% in birds number 2 and 3 while in bird number 1 estimates were 8% apart. Estimates of the proportion of cecal contents emptied may differ as much as 15% for an individual dropping using simultaneous Cr-51 and Ce-144 markers, but generally they were within 6% (table 4).

Weights of cecal contents at the time of emptying were estimated from the proportion 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 at the time of emptying for a total of 14 fill cycles (table 4). Average cecal filling followed a defecation (minimum cecal fill) equalled 0.30 g DM and was calculated as average maximum fill minus average cecal droppings.

TABLE 3. Per cent of cecal contents emptied per cecal defecation in rock ptarmigan as determined by $^{133}BaSO_4$ recovery in cecal droppings (eq. 1).

Cecal defecation	Bird identification 1	2	3	4	5	6	7	8
1	64	78	60	65	42	22	80	82
2	47	47	30	70	37	94	72	80
3	44	46	66	23	46	48	82	42
4	44	33	55	85	52		38	
5	61		56	32	57			
6			57	47				
mean	52(10)[a]	51(19)	54(12)	54(24)	47(8)	55(36)	68(20)	68(23)
mean of means		55(18)						

[a]Mean (standard deviation).

TABLE 4. The weight of cecal droppings, cecal fill and per cent of cecal contents emptied per cecal defecation for rock ptarmigan as determined by Cr-51 and Ce-144 recovery in cecal droppings (eq. 1).

			Cr-51		Ce-144	
Bird no.	Defecation no.	weight of cecal dropping (g DM)	cecal fill at time of emptying (g DM)	contents emptied (%)	cecal fill at time of emptying (g DM)	contents emptied (%)
1	1	0.20	0.51	39	0.57	35
	2	0.49	0.82	60	0.82	60
	3	0.35	0.62	56	0.71	49
	4	0.58	0.89	65	1.14	51
	5	0.31	0.79	39	1.29	24
mean		0.39 (0.15)[a]	0.73 (0.16)	52 (12)	0.91 (0.30)	44 (14)
2	1	0.32	0.62	52	0.59	54
	2	0.23	0.49	47	0.51	45
	3	0.35	0.58	60	0.59	59
	4	0.42	0.66	64	0.76	55
	5	0.12	0.36	33	0.41	29
mean		0.20 (0.12)	0.54 (0.12)	51 (12)	0.57 (0.13)	48 (12)
3	1	0.54	0.65	83	0.62	87
	2	0.35	0.51	68	0.49	71
	3	0.39	0.51	76	0.54	72
	4	0.41	0.64	64	0.83	49
mean		0.42 (0.08)	0.58 (0.08)	73 (8)	0.62 (0.15)	70 (16)
mean of means		0.36 (0.13)	0.62 (0.14)	59 (14)	0.70 (0.25)	54 (17)

[a]Mean (standard deviation).

Figure 3 summarizes the mean filling and emptying cycle of rock ptarmigan in the present study. The rate of cecum fill was calculated as the rate of cecal feces output plus that proportion 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. 1975). Therefore the fill rate of the cecum was 0.042 x 1.19 or 0.05 g DM/hr.

Turnover of Cecal Contents

A comparison of specific activities versus time curves for Cr-51 and Ce-144 in cecal droppings are shown in figure 2. The biological half time ($t_{1/2}$) of these lines, the time required for the specific activity (μCi/g DM) to decrease by 50%, was invariably less for Cr-51 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 Cr-51 would have passed through the cecum. Thus an average of between 62 and 65% of the cecal contents would have emptied during an 8.6 hour period. Both estimates are higher than estimated by equation 1 for the markers Ce-144, Ba-133 and Cr-51, respectively.

Figure 4 shows that the $t_{1/2}$ for Ce-144 and Cr-51 in the cecum declined linearly with the mean fraction of cecum emptied per defecation.

FIGURE 2. The elimination of liquid (^{51}Cr-EDTA) and dry matter (Ce-144) markers from the cecum of rock ptarmigan.

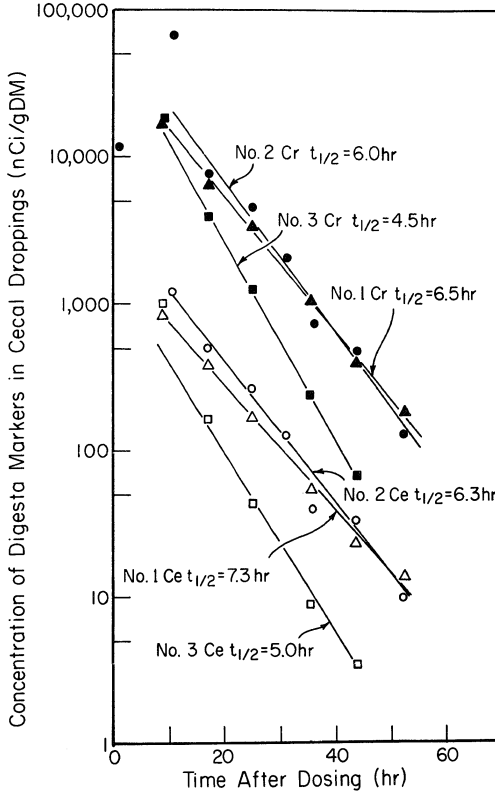


FIGURE 3. Mean cecum filling and emptying cycle in 3 rock ptarmigan. The fill rate was calculated from the DM excretion rate adjusted for digestibility (19%, see text) of cecal contents.

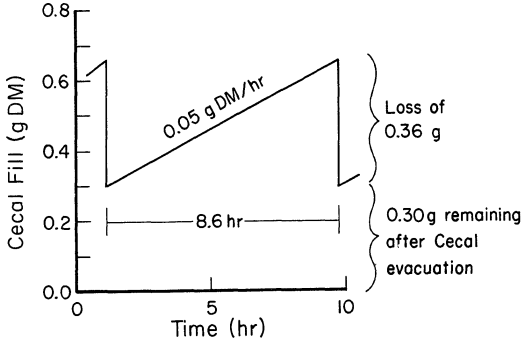
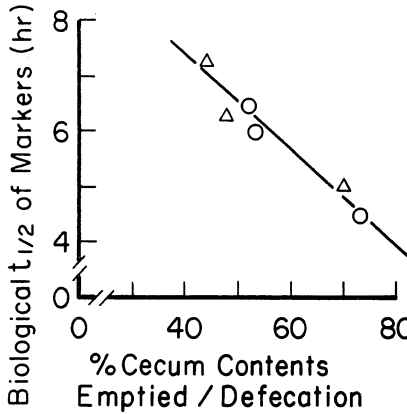


FIGURE 4. The relationship between markers half-time (○, ^{51}Cr-EDTA and Δ, Ce-144) in the cecum and the per cent of cecum contents emptied per cecal defecation for the rock ptarmigan.



DISCUSSION

In the present studies it was 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 organic matter, that $^{144}CeCl_3$ can be used 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 hours (table 2). The TT of liquid and particulate phases of 1-1.5 hr 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 as Downes and McDonald (1964) have shown that up to 4.7% of ingested Cr-51 may be absorbed from the alimentary tract of the sheep. Since no ^{51}Cr-EDTA diffuses from the blood stream to the alimentary tract, 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 liquid through the intestines, the first appearance of ^{51}Ce-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 hours, 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), it was concluded 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 estimate for entry of cecal dry matter may be obtained following continuous dosing of Ce-144 and when this was done in a separate study on captive rock ptarmigan, the average entry of particulate matter was slightly higher (18%) than the present estimate of 13% (Gasaway et al. 1975). Extrapolation from these data to the field must be done with caution as the proportion 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 (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 proportion of DM entering the cecum. The smaller cecum size for captive than wild ptarmigan is consistent with findings by Moss (1972) for the red grouse. 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 atrophy of the cecum.

From the high recoveries (95-97%) of ^{51}Cr-EDTA in cecal droppings of undisturbed birds (table 1), it is concluded that a high proportion

of liquid and suspended material which reaches the I-C-C region is diverted into the cecum. Morphological studies indicate that the opening into the cecum is very small and combined with present observations of low entry of particulate matter into the cecum, it is inferred that the cecal valve 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. 1975) it has been found that 86% of the liquid fraction enters the cecum when ^{51}Cr-EDTA is administered continuously over a 3 day period. A small proportion 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.

A model of the cecal filling and emptying process is shown in figure 3. In this model it is hypothesized that cecal filling is continuous between evacuations in rock ptarmigan. Evidence supporting this model was deduced from (a) the relatively constant ^{51}Cr-EDTA output in the intestinal droppings in ptarmigan fed a ^{51}Cr-EDTA labeled food, and (b) observations of gut contents in the I-C-C region and the stage of filling of the cecum observed in freshly killed birds.

(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. 1975) and the concentration of Cr-51 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 potentially would have entered the cecum was diverted down the colon, a periodic large increase in Cr-51 concentration would be expected in intestinal droppings. This latter phenomenon was not noted, hence, the data suggest that cecal filling is a continuous one way flow followed by periodic emptying to form a cecal dropping.

(b) It has been 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 were similar to that 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 apparently filled 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 Askester et al. (1967) and Skadhauge (1968) and is the result of antiperistaltic movements. Askester et al. (1967) and Hill (1971) suggest retrograde flow may provide more efficient recovery of electrolytes, water and nutrients and provide a nitrogen source for cecal microbes. Fenna and Boag (1974) observed antiperstolic waves in the large intestine which continued into the cecum of Japanese quail,

Coturnix coturnix, however they did not observe material moving anteriorly in the large intestine and entering the cecum. Moss and Parkinson (1972) failed to find uric or ornithuric acid in cecal droppings of red grouse upon quantitative chemical analysis which indicates that urine did not enter the cecum. Thus, retrograde flow of urine in red grouse probably does not occur and no evidence has been found by us for retrograde flow in the rock or willow ptarmigan.

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 because of their larger surface to volume ratio. The mean retention time of material entering the cecum and hence the mean time digesta was exposed to bacterial digestion and fermentation was approximately 6 hours (fig. 2). However, a small amount of digesta remains in the cecum for up to 24 hours. The duration particles remained in the cecum varies between individual birds and the retention time decreased as the mean percentage emptied per defecation increased (fig. 4). Whereas, 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 a highly efficient and light weight ceca. The important component in maintaining a minimal sized ceca which allows 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 empty in rapid succession based on the observation that wild birds had nearly equal volumes of contents in both ceca suggesting filling and emptying were carried out in phase. Also, captive ptarmigan produced two cecal droppings of about equal volume each time the cecum was emptied; presumably each is from a separate pouch.

Three markers used to estimate the per cent cecal contents emptied per dropping indicated that between 54% and 59% of the total contents were voided per cecal defecation (table 3 and 4). The remaining contents retained in the cecum (fig. 3) presumably provided a ready reservoir of innoculum for new material thus minimizing the lag time while bacterial numbers increased.

A comparison of minimum and maximum fill of shot wild rock ptarmigan (Gasaway 1975a) observed in a day 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 cecal emptying 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 (table 4) suggesting the level of fill was not the critical factor initiating cecal defecation. Estimates of maximum cecal fill ranged from 0.36 to 1.29 mean of 0.66g DM (fig. 3). If either the available space within the 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) suggests 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. 1975) cecal droppings per day, respectively. Apparently a variety of 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 cecal fill was a minor factor in initiating cecal discharge.

It was hypothesized that the cecum fills continuously between cecal defecations and that no evidence for cecal filling from retrograde flow was found for rock ptarmigan. Contents retained in the cecum after defecation presumably provided 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.

LITERATURE CITED

AKESTER, A. R., R. S. ANDERSON, K. J. HILL, AND G. W. OSBALDISTON. 1967. A radiographic study of urine flow in the domestic fowl. Br. Poult. Sci. 8:209-215.

BROWNE, T. G. 1922. Some observations on the digestive system of the fowl. J. Comp. Pathol. Ther. 35:12-32.

DOWNES, A. M., AND I. W. McDONALD. 1964. The chromium-51 complex of ethylenediamine tetraacetic acid as a soluble rumen marker. Br. J. Nutr. 18:153-162.

DUKE, G. E., G. A. PETRIDES, AND R. K. RINGER. 1968. Chromium-51 in food metabolizability and passage rate studies with the ring-necked pheasant. Poult. Sci. 47:1356-1364.

ELLIS, W. C., AND J. E. HUSTON. 1968. ^{144}Ce-^{144}Pr as a particulate digesta flow marker in ruminants. J. Nutr. 95:67-78.

FENNA, L. AND D. A. BOAG. 1974. Filling and emptying of the caecum. Can. J. Zool. 52:537-540.

GASAWAY, W. 1975a. Volatile fatty acid production and metabolizable energy derived from cecal fermentation in rock ptarmigan. In prep.

GASAWAY, W. 1975b. Volatile fatty acid production and metabolizable energy derived from cecal fermentation in willow ptarmigan. In prep.

GASAWAY, W., D. HOLLEMAN, AND R. WHITE. 1975. Dry matter digestion and water absorption in the intestine and cecum of rock ptarmigan. In prep.

GROVUM, W. L., AND G. D. PHILLIPS. 1973. Rate of passage of digesta in sheep. 5. Theoretical considerations based on a physiological model and computer simulation. Br. J. Nutr. 30:377-390.

HILL, K. J. 1971. The physiology of digestion, p. 25-49. In D. J. Bell and B. M. Freeman [eds.] Physiology and Biochemistry of the domestic fowl. Vol. I. Academic Press, N.Y.

INMAN, D. L., AND R. K. Ringer. 1973. Differential passage of cellulose and $^{51}CrCl_3$ in three non-domestic gallinaceous species. Poult. Sci. 52:1399-1405.

McBEE, R. H., AND G. C. WEST. 1969. Cecal fermentation in the willow ptarmigan. The Condor 71:54-58.

MOSS, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Mgmt. 36:99-104.

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.

NECHAY, B. R., S. BOYARSKY, AND P. CATACUTAN-LABAY. 1968. Rapid migration of urine into intestine of chickens. Comp. Biochem. Physiol. 26: 369-370.

RÖSELER, M. 1929. The Bedeutung der Blinddärme des Haushuhns für die Resorption der Nahrung und die Verdauung der Rohfaser. Z. Tierzucht Züchtungsbiol. 13:281-310.

SKADHAUGE, E. 1968. The cloacal storage of urine in the rooster. Comp Biochem. Physiol. 24:7-18.

VONK, H. J., AND N. POSTMA. 1949. X-ray studies on the movements of the hen's intestine. Physiologia Comp. Oecol. 1:15-23.

CHAPTER II.

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

INTRODUCTION

Despite the many investigations of hindgut functions in avian species (Sturkie 1965; Hill 1971; Hudson et al. 1971; Jayne-Williams and Fuller 1971; Ziswiler and Farner 1972), incomplete information of digestive function still exists. Primary hindgut functions appear to be microbial digestion of carbohydrate and protein, absorption of end products of hindgut fermentation, water, some minerals, and microbial synthesis of vitamins. The cecum of all herbivores is the main fermentation organ of the hindgut and in avian species attains its greatest size in the family Tetraonidae (grouse and ptarmigan). The avian cecum is analogous in function to ceca of herbivorous mammals and has many functional similarities to the rumen. Well developed ceca increase the digestive 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 graeca, and bobwhite quail, Colinis virginianus (Inman 1973; Inman and Ringer 1973) and in rock ptarmigan, Lagopus mutus (Gasaway unpub.). Dry matter (DM) absorption in the ceca of ruffed grouse, chukar and bobwhite quail was estimated and compared to intestinal absorption by Inman (1973). Bacterial digestion and fermentation of carbohydrates and proteins in the cecum yield volatile fatty acids (VFA) 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 rock ptarmigan can be recovered in exhaled CO_2, it is clear that energy is derived from dietary cellulose (Gasaway unpub.).

Other functions, including water and electrolyte absorption 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 also 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, flow routes of water, water soluble materials and particulate dry matter components of digesta through the hindgut were determined and the absorption of DM and water was estimated.

MATERIALS AND METHODS

The 4 birds used in the ^{51}Cr-EDTA and Ce-144 trials were 1.5 year old rock ptarmigan 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 hours. Five days prior to the experiment the birds were placed in individual wire mesh (1.3 x 2.5 cm) 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 water absorption in the large intestine.

Labeled (^{51}Cr-EDTA and Ce-144) food was substituted for unlabeled food 24 hours prior to the experimental period in order to allow for the equilibration of the marker in the gut. Excreta was 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 hours in plastic vials and weighed to determine excreta output. Samples were radio assayed and marker concentration was calculated.

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

Water loss via excreta was estimated from the water content of periodically collected fresh dropping. Cecal and intestinal excreta were dried at 80°C for 24 hours to determine moisture content.

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

Digestibility of the diet, over a 3 day period, was determined by the total collection method (Kleiber 1961) as follows:

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

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) as follows:

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

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

Estimates of water absorption in the large intestine were made by determining the difference in the proportion of water in proximal and distal large intestinal contents (Grovum and Williams 1973a). Contents from the proximal and distal colon were collected and placed in tared glass vials and the moisture content was determined by drying at 80° for 24 hours. It was assumed that no dry matter was absorbed in the colon, thus the reduction in g water/g DM between the proximal and the distal end of the colon was equal to the water absorbed. Small amounts of electrolyes are absorbed in the large intestine, however the error induced was considered insignificant.

Preparation of ^{51}Cr-EDTA was 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 11.2 g DM per day, respectively (table 1). Cecal droppings averaged 15% of total excreta DM loss (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 digestibility estimates from the ratio methods were significantly different ($P<0.05$), but neither differed significantly from the estimates based on the total collection.

Estimates for short time intervals using the $^{144}CeCl_2$ ratio method followed a daily cyclic pattern in which digestibility reached a peak near 1600 hours and declined throughout the night until mid-morning (fig. 1). High digestibility coincided with periods of highest rates of intestinal excreta output.

Digestion in the Cecum

The average specific activities 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 food material entering the cecum (eq. 2).

Pattern of Marker Excretion in Intestinal and Cecal Excreta

Ce-144 specific activity in intestinal droppings showed diurnal

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)
Cr-51	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	62.0	60.4 (2.2)
Cr-51 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)
Cr-51	87.0	85.1	87.2	85.4	86.4 (0.8)

[a]Mean (standard deviation).

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

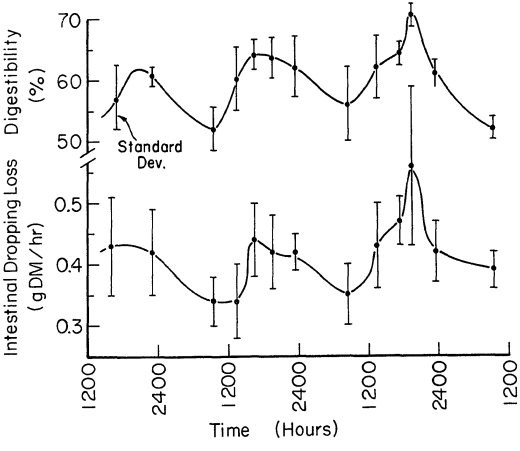
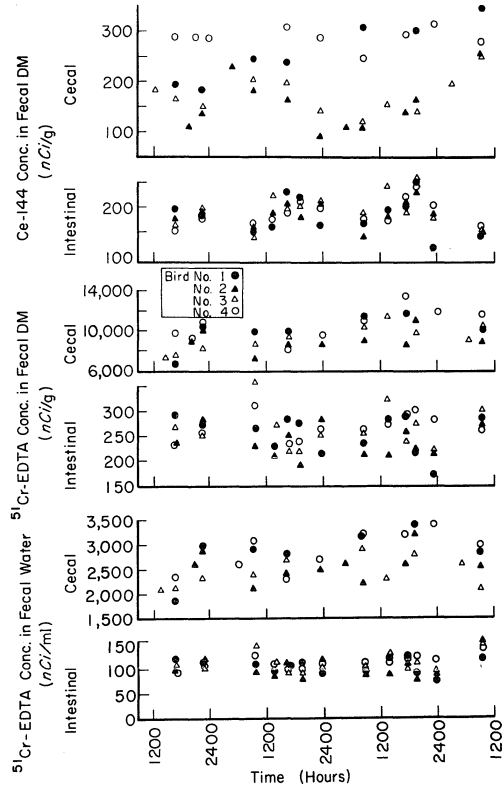


FIGURE 2. The concentration of markers in dry matter and water of cecal and intestinal droppings from 4 rock ptarmigan fed a diet labeled with Ce-144 and ^{51}Cr-EDTA.



oscillations and averaged 2.5 times greater than specific activity of the food (fig. 2). Specific activity of Ce-144 in cecal excreta averaged 1.2 times greater than intestinal excreta and showed no diurnal pattern (fig. 2). Ce-144 specific activity 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 specific activity in cecal excreta also shunted the lowest proportion 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 Cr-51 was accounted for in cecal droppings (table 1). This diversion to the cecum accounted for the low Cr-51 concentration in intestinal droppings. Thus, ^{51}Cr-EDTA could not be used to estimate DM digestion; it is strictly a liquid rather than a DM marker.

Water Absorption, Loss and ^{51}Cr-EDTA Excretion Pattern in Fecal Water

Water loss 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 specific activity of water from cecal droppings was 25.5 times higher than that of intestinal droppings (table 2), reflecting the large proportion of water absorbed from the cecum compared with the large intestine.

Water absorbed from contents of the large intestine of wild rock ptarmigan was estimated to be 12% (table 3) of the water entering the large intestine.

DISCUSSION

Total 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. 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

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)		Relative Cr-51 concentration per ml fecal water
	Cecal dropping	Intestinal dropping	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).

TABLE 3. Water absorbed while passing through the large intestine of wild rock ptarmigan.

ml water entering large intestine per ml water excreted	% water absorbed
1.09	8
1.16	14
1.18	15
1.14(0.05)[a]	12(4)

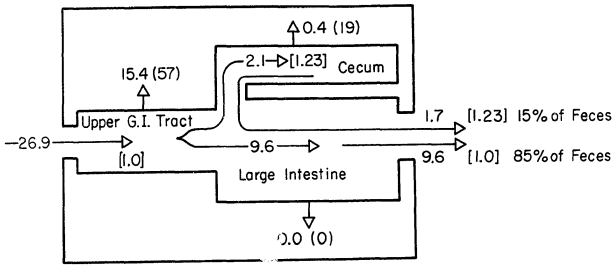
[a]Mean (standard deviation).

of each feces type, otherwise significant errors will result. On the other hand, Ce-144 specific activity 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 $^{51}CrCl_3$.

A model of daily food flow, sites of digestion and DM absorption was constructed from data collected in this experiment and is summarized in figure 3. Construction of 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 was 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 intestinal dropping output of 9.6 g DM/day. Dry weight of urine output was unknown, but probably does not exceed 0.4 g/day for a bird the size of a ptarmigan (Sykes 1971) and if neglected would contribute only a small error to the estimate of fecal output. DM reaching the ileo-cecal-colic (I-C-C) junction equalled the amount entering the cecum (2.1 g/day) plus the weight of intestinal droppings (9.6 g/day) giving a total flow of 11.7 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.

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 digested organ; [ ], relative concentration of Ce-144 in dry matter.

Lagopus mutus



The cecum appeared to play only a minor role in DM digestion in these hand reared, captive rock ptarmigan.

Estimates of DM disappearance 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 Ce-144 into the cecum was the lowest and the DM output from the cecum was the highest recorded in the study. It is suggested 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), the higher proportion of fine particles in the cecum resulted in a spuriously lower Ce-144 specific activity. 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 suggests.

The present 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 the present study, DM digestibility estimates for the cecum using ^{51}Cr-EDTA would be about 97% and this error highlights the importance of choosing markers when

determining DM digestion in specific organs.

Based on the present evidence for separation of liquid and dry matter, a model of operation is proposed for the entry of material into the cecum. It is hypothesized 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. By maintaining a small controlled orifice into the cecum, fluid can be forced into the cecum under hydrostatic pressure. Intermittent remixing of the contents in the I-C-C area and cleaning of the cecal neck orifice would also be necessary to accomplish the high degree of separation seen in the ptarmigan. It has been shown that the cecal filling process is continuous (Gasaway et al. 1975), and it is now necessary to invoke a reasonably constant hydrostatic pressure filtering process. The remaining coarse material is then assumed to be propelled down the large intestine by peristaltic waves. The watery suspension entering the cecum first passes through a 5-8 cm long cecal neck, a heavy wall 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. Fenna and Boag (1974) observed peristaltic and antiperistaltic waves in the small and large intestines, respectively, of Japanese quail, Coturnix coturnix, which converged at the I-C-C junction. They concluded these contractions forced liquids into the cecum. Frequent alternation of peristaltic and antiperistaltic waves in the large intestine would be required to accomplish a more or less continuous cecal fill and the general movement of intestinal contents

down the gut.

Present findings for cecal DM digestion 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) and confirms 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. Captive birds digested 2.5% of the digested DM in the cecum, whereas, the energy available from cecal fermentation in wild birds was 7% of the free living energy requirements (Gasaway 1975a) or about 3 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 high quality diet, 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. From this we conclude atrophy 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

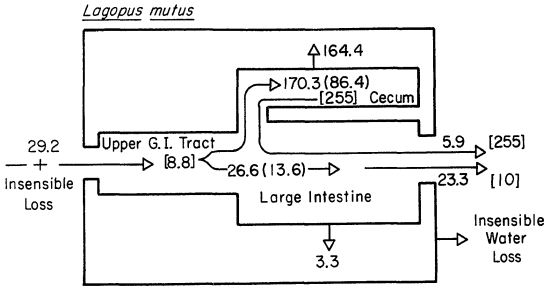
requirements.

In spite of the reduced DM fill in ceca of captive birds, the cecum retains a high efficiency for water absorption. 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 water loss from intestinal droppings was 23.3 ml/day. Assuming a water absorption in the large intestine of 12% for wild birds during winter, 3.3 ml water would be absorbed of the 26.6 ml of water entered 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. The assumption was made 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, 164.4 ml of water per day was absorbed and 98% of all water absorption in the hindgut occurred in the cecum.

The flow and absorption values in figure 4 may also be calculated using the relative ^{51}Cr-EDTA concentration in fecal 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.

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 enter organ; [ ], relative concentration of ^{51}Cr-EDTA in water.



Assuming 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 units at the time of emptying and 5.9 ml of water were lost per day, 1505 μCi Cr-51 would have entered the cecum per day. Concentration of ^{51}Cr-EDTA in water entering the cecum was assumed to be 8.8, therefore 171 ml of water ($\frac{1505}{8.8}$) would have entered the cecum. Both methods of calculation provide similar entry and absorption rates for water in the cecum and indicate 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. These present data support the observation of Duke et al. (1968) who showed that $^{51}CrCl_3$ concentration in cecal droppings was about 2 times greater than that of intestinal droppings in pheasants. Also Inman and Ringer (1973) reported 33% and 19-29% of $^{51}CrCl_3$ is recovered in cecal droppings from chukars and bobwhite quail, respectively. Apparently, the relative effectiveness and importance of cecal water absorption in these bird species is less than in rock ptarmigan and the large intestine plays an increasing role. Therefore, these data also infer 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 in which little fermentation occurs (Ziswiler and

Farner 1972; Moss 1972; Gasaway, unpubl.).

SUMMARY

The flow routes of water and DM through the hindgut were determined and the absorption of DM and water were estimated in captive rock ptarmigan using radioisotopic markers ^{51}Cr-EDTA and $^{144}CeCl_3$.

At the I-C-C junction soluble and very fine particulate DM was diverted into the cecum while coarse material was passed down 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 DM digestion 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. It was 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.

It was hypothesized that liquid and suspended DM entered the cecum under hydrostatic pressure generated by the contraction of the small and large intestine in the ileo-cecal-colic region. Maintenance of a small controlled orifice in the cecal valve 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.

LITERATURE CITED

ANNISON, E. G., K. J. HILL, AND R. KENWORTHY. 1968. Volatile fatty acids in the digestive tract of the fowl. Br. J. Nutr. 22:207-216.

DOWNES, A. M., AND I. W. McDONALD. 1964. The chromium-51 complex of ethylenediamine tetraacetic acid as a soluble rumen marker. Br. J. Nutr. 18:153-162.

DUKE, G. E., G. A. PETRIDES, AND R. K. RINGER. 1968. Chromium-51 in food metabolizability and passage rate studies with the ring-necked pheasant. Poult. Sci. 47:1356-1364.

FENNA, L., AND D. A. BOAG. 1974. Filling and emptying of the cecum. Can. J. Zool. 52:537-540.

GASAWAY, W. 1975a. Seasonal volatile fatty acids production and metabolizable energy derived from cecal fermentation in rock ptarmigan. In prep.

GASAWAY, W. 1975b. Volatile fatty acid production and metabolizable energy derived from cecal fermentation in willow ptarmigan. In prep.

GASAWAY, W., D. HOLLEMAN, AND R. WHITE. 1975. Digesta flow in the intestine and cecum of the rock ptarmigan. In prep.

GROVUM, W. L., AND V. J. WILLIAMS. 1973a. Rate of passage of digesta in sheep. 1. The effect of level of food intake on marker retention times along the small intestine and on apparent water absorption in the small and large intestines. Br. J. Nutr. 29:13-21.

HALNAN, E. T. 1949. The architecture of the avian gut and tolerance of crude fiber. Br. J. Nutr. 3:245-253.

HENNING, H. T. 1929. Die Verdaubichkeit der Rohfaser beim Huhn. Landwirt. Vers. sta 180:253-286.

HILL, K. J. 1971. The physiology of digestion, p. 25-49. In D. J. Bell and B. M. Freeman [eds.] Physiology and Biochemistry of the Domestic Fowl. Vol. I. Academic Press, New York.

HUDSON, D.A., R. J. LEVIN, AND D. H. SMYTH. 1971. Absorption from the alimentary tract, p. 51-71. In D. J. Bell and B. M. Freeman [eds.] Physiology and Biochemistry of the Domestic Fowl. Vol. I. Academic Press, New York.

INMAN, D. L. 1973. Cellulose digestion in ruffed grouse, chukar partridge, and bobwhite quail. J. Wildl. Mgmt. 37:114-121.

INMAN, D. L., AND R. K. RINGER. 1973. Differential passage of cellulose and $^{51}CrCl_3$ in three non-domestic gallinaceous species. Poult. Sci. 52:1399-1405.

INMAN, D. L., G. A. PETRIDE, AND R. K. RINGER. 1969. Chromium-51 digestive studies of avian species. Proc. Poult. Sci. Assoc. 48:1826. (abstract)

JAYNE-WILLIAMS, D. J., AND R. FULLER. 1971. The influence of the intestinal microflora on nutrition, p. 73-92. In D. S. Bell and B. M. Freeman [eds.] Physiology and Biochemistry of the Domestic Fowl. Vol. I. Academic Press, New York.

KLEIBER, M. 1961. The Fire of Life. An introduction to animal energetics. John Wiley and Sons, Inc. N. Y., London.

McBEE, R. H., AND G. C. WEST. 1969. Cecal fermentation in the willow ptarmigan. The Condor 71:54-58.

MOSS, R. 1972. Effects of captivity on gut lengths in red grouse. J. Wildl. Mgmt. 36:99-104.

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.

NECHAY, B. R., AND B. D. C. LUTHERER. 1968. Handling of urine by cloaca and ureter in chickens. Comp. Biochem. Physiol. 26:1099-1105.

PARHON, C. C., AND E. BARZA. 1967. Recherches sur l'absorption caecale chez les oiseaux domestiques. Rev. Roum. Biol.-Zoologie 12:109-115.

RADEFF, T. 1928. Über die Rohfaserverdauung beim Huhn und die hierbei dem Blinddarm zukommende Bedeutung. Biochem. Z. 193:192-196.

SCHMIDT-NEILSEN, K., A. BORUT, P. LEE, AND E. CRAWFORD, JR. 1963. Nasal salt excretions and the possible function of the cloaca in water conservation. Science 142:1300-1301.

SIBBALD, I. R., J. SUMMERS, AND S. SLINGER. 1960. Factors affecting the metabolizable energy content of poultry feeds. Poult. Sci. 39:544-556.

SKADHAUGE, E. 1967. In vivo perfusion studies of the cloacal water and electrolyte resorption in the fowl (Gallus domesticus). Comp. Biochem. Physiol. 23:483-501.

SKADHAUGE, E. 1968. The cloacal storage of urine in the rooster. Comp. Biochem. Physiol. 24:7-18.

STURKIE, P. D. 1965. Avian Physiology, p. 766. Cornell University Press, Ithaca, New York.

SUOMALAINEN, H., AND E. ARHIMO. 1945. On the microbial decomposition of cellulose by wild gallinaceous birds (family Tetraonidae). Ornis Fenn. 22:21-23.

SYKES, A. 1971. Formation and composition of urine, p. 233-278. In D. J. Bell and B. M. Freeman [eds.] Physiology and Biochemistry of the Domestic Fowl. Vol. I. Academic Press, New York.

THORNBURN, C. C., AND J. S. WILLCOX. 1965a. The caeca of the domestic fowl and digestion of the crude fibre complex. I. Digestibility trials with normal and caecectomised birds. Br. Poult. Sci. 6:23-31.

THORNBURN, C. C., AND J. S. WILLCOX. 1965b. The caeca of the domestic fowl and digestion of the crude fibre complex. II. Experiments in vivo with fistulated birds, and the artificial and isolated caecum in vitro. Br. Poult. Sci. 6:33-43.

ZISWILER, V., AND D. S. FARNER. 1972. Digestion and the digestive system, p. 343-430. In Avian Biology. Vol. II. Academic Press, New York.

CHAPTER III.

SEASONAL VARIATION IN DIET, VOLATILE FATTY ACID PRODUCTION AND SIZE OF THE CECUM OF ROCK PTARMIGAN

INTRODUCTION

Rock ptarmigan, Lagopus mutus, live throughout the year in the arctic and subarctic of North America and Eurasia. They consume a fibrous diet year round which is composed of leaves, seeds and berries during spring through autumn and buds and catkins during winter (Weeden, 1969). Rock ptarmigan, as other members of the family Tetraonidae, have morphologically and physiologically adapted to these relatively low quality foods through the development of large ceca which increase digestive efficiency. In ptarmigan, the ceca are long, paired sac-like extensions of the gut which originate between the large and small intestine. Digesta is separated into two fractions at the ileo-cecal-colic (I-C-C) junction. The fluid phase, consisting of liquid and suspended fine particles, is diverted into the ceca where it is exposed to bacterial fermentation. The coarse, woody phase is passed along the relatively short colon and is excreted as dry fiberous droppings (Leopold, 1953; Moss & Parkinson, 1972; Gasaway et al., 1975b). The cecum functions as a "fermentation vat" where complex carbohydrate molecules and other nutrients which escape absorption in the small intestine may be digested, fermented and absorbed. Bacterial numbers as high as 10^{11}/g cecal contents were found in willow ptarmigan, Lagopus lagopus (McBee & West, 1969), and end products of their fermentive processes which can be used as energy sources by the avian host are primarily acetate, propionate, butyrate and ethanol (Annison et al., 1968; McBee & West, 1969; Moss & Parkinson, 1972; Gasaway, 1975). These fermentation products provide

an average of 11% of the standard metabolic rate and about 4% of the estimated free living energy needs for willow ptarmigan during winter (Gasaway, 1975).

It was hypothesized that cecal digestion and fermentation may play a more important nutritional role during winter when food quality was lowest and cecal size was greatest, and a study was initiated which would evaluate cecal fermentation during five periods of the year.

MATERIALS AND METHODS

Protocol

Seventy rock ptarmigan in total were shot during April, July, August, September and October on Eagle Summit, Alaska (65°30' N lat.; 145°25' W long.) and Ester Dome (15 miles northwest of Fairbanks, 64° 53' N lat.; 148°4' W long.) during November and December between 1970 and 1972.

Birds shot during September through April were immediately taken to a warm truck where cecal content sampling was carried out. During July and August, volatile fatty acids (VFA) sampling equipment was carried in a backpack allowing for immediate processing of the bird. Body weight was recorded and the cecum removed from the bird, weighed with contents and the length measured. The cecum was then opened and contents transferred to a glass vial, incubated, periodically sampled and specimens preserved. Cecal tissue was weighed after contents

were removed. Preserved cecal contents were later analyzed for concentrations and composition of VFA. Cecal contents of these birds by the sum of all sample weights. Age and sex of birds were determined (Weeden, 1961) and crop contents were removed and saved for chemical and taxonomic analysis. The total time required to complete the sampling of 1 bird was approximately 30 minutes. Thirty-two of the ptarmigan were shot to provide a larger sample for physical measurements of cecum size and crop contents.

Chemical methods

Dietary nutrients: Crude protein in food was determined by the Kjeldahl method (Hawk et al., 1954). Neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin and cellulose were determined in crop contents by the Van Soest forage fiber analyses methods (Goering & Van Soest, 1970). Lipid content of dry food was determined by extraction using petroleum ether (30-60°C boiling point) in a Soxhlet extractor.

In vitro incubation and sampling of cecum contents: Cecum contents were removed from both ceca and put in a 20 cc screw cap glass vial filled with CO_2. Contents were mixed and the first subsample (approximately 1 g) was taken 6-12 minutes after death. The vial was flushed with CO_2, tightly capped and incubated in a water bath maintained between 38 and 40°C. Four subsamples were taken at approximately 5 minute intervals and the vial flushed with CO_2 following each subsample. The 1 g subsamples of fresh contents were transferred to preweighed vials (20 ml capacity)

containing 5 ml of 1 N HPO_3 to stop all bacterial fermentive action. The vials were stored frozen until analyzed for VFA. Weight of the subsample was determined by difference after reweighing the vial.

Quantitative analysis of VFA: The weighed samples of cecal contents in meta-phosphoric and were rinsed into a centrifuge tube and the volume brought up to 15 ml with distilled water. Sediment was spun down and supernatant liquid decanted for VFA analysis. Total VFA was estimated by steam distillation as described by Gray & Stevens (1966) using a Markhan type still. Four 50 ml distillate samples were tritrated with 0.01 N NaOH to a brom-thymol blue endpoint (pH 7-7.6) in a CO_2 free atmosphere. VFA concentration was corrected for 90% recovery in distillation. Potassium salts of VFA were obtained by adding excess KOH (pH>9) and evaporating to dryness. Samples of the salts were analyzed for molar proportions of VFA by in a Hewlett-Packard Model 402 gas chromatograph. The salts were redissolved in 0.1-0.3 ml water and 0.5-10 µl were injected into the column under one of the following two sets of conditions: either a 6 foot, stainless steel column (0.25 inch I.D.) packed with 10% FFAP-Chromosorb W was used with helium as carrier gas and the flame ionization detector injection port and oven temperatures at 250, 250 and 200°C, respectively; or, a 6 foot, stainless steel column (0.125 inch I.D.) packed with SP-1200 Chromosorb W was used with helium as carrier gas and temperatures for the oven, flame ionization detector and injection port at 130, 200, 180°C, respectively.

Calculation of VFA production rates and metabolizable energy in VFA: VFA production was determined by the "zero time" method from the

slope of the least squares linear regression line of individual VFA concentration (μM/g fresh contents) versus time in minutes after death (Caroll & Hungate, 1954). Production of acetic, propionic and butyric acids were calculated for each bird. Total VFA production (μM/g fresh contents•min) was determined as above using total VFA concentration. Initial concentration of VFA (μM/g fresh contents) in cecal contents at time of death was estimated from the y intercept of the total VFA production regression line.

The production of VFA/bird (mM/min) was calculated by multiplying the mM/g•min times cecal contents. VFA production for a 24 hour period (mM/day) was estimated by multiplying mM/min times minutes/day.

Metabolizable energy of each VFA was calculated from the caloric value of its heat of combustion. Heats of combustion of acetate, propionate and butyrate were taken as 209.4, 367.2 and 524.3 kcal/mole, respectively (Hodgman et al., 1958). Therefore, the ME of VFA produced in the cecum per day was equal to moles of each VFA produced times its respective caloric value.

Statistical analysis followed procedures given in Steel & Torrie (1960) for analysis of variance and Duncan's new multiple range test.

RESULTS

Analysis of crop contents collected from late September through December and April indicate ptarmigan were feeding predominately on

buds and catkins of dwarf birch, Betula nana (Table 1). Berries were consumed during this period when plants were free of snow cover (September-October and April). Few willow buds, Salix, were found in crops during fall and winter while aspen buds, Populus tremuloides, were consumed in a relatively high proportion, 26% during November and December by birds on Ester Dome.

The greatest variety of plant parts and species were found in the crop during July. Seed pods of Pedicularis and bulbils of Polygonum viviparum represented about 64% of the crop contents while the remaining portion was made up of a wide variety of seeds, berries and leaves (Table 1). During August leaves of Oxytropis, 51%, Dryas, 17% and Salix, 12%, were consumed in greatest abundance while seeds, leaves, buds, catkins and berries of many other species were also selected (Table 1).

Mean crop fill was lowest in birds shot during July, 0.7 g dry matter (DM), when it was light 24 hours/day whereas during the November-December collection period when daylight limited the feeding period, crop fill was highest, 6.3 g DM. Crop fill between 1.7 and 3.0 g DM was found during the other seasons. These data support the previous studies by Irving et al. (1967) which showed the weight of crop contents in willow ptarmigan increase as the daylight decreases from July to December and crop contents decrease as the daylight increases from January to June.

The seasonal pattern of nutrient composition in crop contents indicates food was most nutritious during the period May through

TABLE 1. Percentage of food items in crops from 47 rock ptarmigan collected in interior Alaska

Food item	April	July	Aug.	Sept.-Oct.	Nov.-Dec.
Unidentified Moss (capsule)	0	2.8	0	0	0
Polystrichum spp. (capsule)	0	3.9	0	0	0
Carex spp. (seed pod)	0.3	0.2	0.2	0.8	0
Luzula multiflora (seed head)	0	1.4	1.7	0	0
Populus tremuloides (bud)	0	0	0	0	25.6
Salix spp. (bud)	6.8	0.1	0.2	2.9	0
Salix spp. (twig)	0.1	0	0	0	0.6
Salix spp. (leaf)	0	1.1	11.6	0	0
Betula spp. (bud)	39.8	2.1	8.4	12.8	42.8
Betula spp. (twig)	3.3	0	0	0.2	9.4
Betula spp. (leaf)	0	0	0.2	0	0
Betula spp. (catkin)	6.2	3.9	0.5	69.1	21.6
Polygonum viviparum (bulbil)	0	39.4	0	0	0
Minuartia arctica (seed head)	0	0.7	0.5	0	0
Anemone narcissiflora (seed pod)	0	0.4	0	1.1	0
Papaver macounii (leaf)	0	0	2.7	0	0
Dryas octopetala (leaf)	3.8	1.8	16.6	0	0
Oxytropis spp. (leaf)	0	3.3	50.8	0	0
Empetrum nigrum (berry)	35.2	8.7	1.2	0	0
Cassiope tetragona (seed capsule)	0	0.1	0	0	0
Vaccinium uliginosum (leaf)	0	2.1	0	0	0
Vaccinium uliginosum (berry)	1.7	0	2.7	9.3	0
Vaccinium vitis-idaea (berry)	2.6	1.5	1.7	0	0
Pedicularis spp. (seed pod)	0	24.5	1.0	0	0
Unidentified (seed)	0	2.1	0	0	0
Unidentified (leaf)	0	2.1	0	0	0
g DM/crop	1.7	0.7	2.0	3.0	6.3
Number of crops	10	12	9	9	7

August and least nutritious the remainder of the year. Crude protein (N X 6.25) was high in growing plants selected during summer and early fall, 23 and 18%, respectively, and low in foods consumed from late fall through winter, 10-14% (Fig. 1). The cell wall component, neutral detergent fiber (NDF), in food varied only a few per cent throughout the year, however the proportions of hemicellulose, cellulose and lignin which make up NDF varied significantly between collection periods. Hemicellulose (NDF-ADF) and cellulose were high during July and August, declined in September and remained low throughout the winter, whereas lignin varied inversely to cellulose (Fig. 1). Lignification of the cell wall was greatest during late fall and winter when the diet was composed chiefly of mature plant portions, buds and catkins (Fig. 1).

Insufficient quantities of most plant species were present in crops of ptarmigan to provide adequate samples for nutrient analysis, hence only the composition of selected food items from crops are shown in Table 2. Birch buds and catkins which are the main winter food of rock ptarmigan were 13-15% crude protein and contained highly lignified cell walls. Buds of birch and aspen contained 19 to 20% ether soluble material whereas all other plants analyzed were from 2 to 8%. Empetrum and Vaccinium berries contained the least protein of foods analyzed, however they provide a good source of soluble cell contents.

Mean body weight varied seasonally between 385 g during August to 435 g in September-October and November-December collection periods.

FIG. 1. Seasonal variation in nutrient composition of crop contents collected from rock ptarmigan in interior Alaska. NDF is nutrient detergent fiber and ADF is acid detergent fiber.

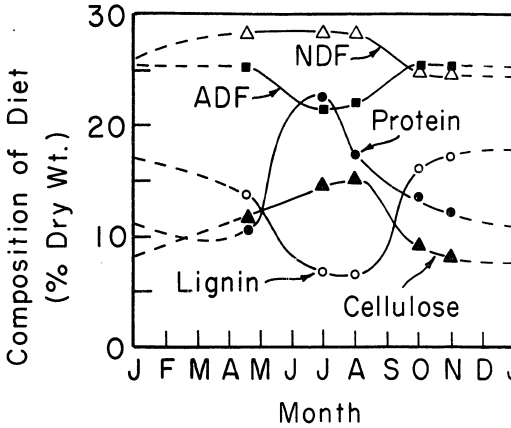


TABLE 2. Composition (per cent dry weight) of some major food items from the crops of rock ptarmigan in interior Alaska

Collection period	Food item	Crude* protein	Lipid	Neutral detergent fiber (NDF)	Acid detergent fiber (ADF)	Lignin	Cellulose
April	Betula (bud)	13.3	18.6	24.9	21.6	14.6	7.0
	Empetrum nigrum (berry)	5.1	5.5	37.0	30.8	15.7	15.2
July	Polygonum viviparum (bulbils)	25.1	2.3	24.0	16.6	5.3	11.3
Sept.-Oct.	Betula (catkin)	15.1	5.9	25.0	28.7	19.3	9.4
	Betula (bud)	13.0	18.6	21.9	22.3	20.8	7.4
	Vaccinium uliginosum (berry)	8.5	--+	15.6	14.6	5.7	8.9
Nov.-Dec.	Betula (catkin)	13.1	8.2	23.9	28.8	20.4	8.4
	Betula (twig)	9.6	--	37.0	33.5	26.9	6.6
	Populus tremuloides (bud)	12.2	20.2	21.4	22.3	13.3	8.9

*Crude protein = % nitrogen x 6.25.

+Not analyzed.

The August collection contained several juvenile birds which were slightly lower in weight than adults thus reducing the overall average. Males and females were pooled since inadequate samples of females were obtained during some seasons. Combining males and females did not appear to alter significantly the patterns of seasonal changes in cecum size and fill which are reported.

The combined length, weight of contents and tissue weight of the cecum were greatest during winter collections, declined to the shortest and lightest state during summer and early fall and again increased as winter approached (Fig. 2). Cecum contents and total cecum weight expressed as a per cent of body weight fluctuated seasonally in a pattern similar to the cecum per se since body weight remained relatively stable compared with the magnitude of change noted in the cecum (Fig. 2).

Molar percentages of acetate, propionate and butyrate in the first sample of cecal contents varied significantly ($P<0.05$) among seasons (Table 3). However no consistant pattern of VFA proportions that could be related to the chemical composition of the food was evident. Therefore, all seasons were pooled and the overall mean molar percentage of acetate, propionate and butyrate was found to be 70.4, 21.5 and 8.0%. Isobutyrate, valerate and isovalerate were found only in trace amounts and therefore are not included in the report.

Production rates of acetate, propionate and butyrate in whole cecal contents ($\mu M/g \cdot min$) are shown in Table 4. Acetate was produced in the greatest quantities followed by propionate and butyrate during

FIG. 2. Seasonal variation in body weights, fill and size of the cecum in rock ptarmigan collected in interior Alaska. Vertical lines indicate 1 standard deviation, numbers in parenthesis are sample sizes.

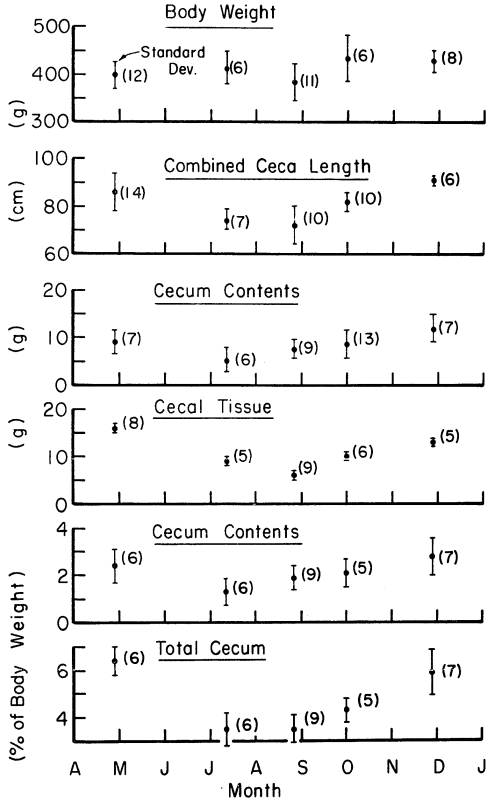


TABLE 3. Mean molar percentages of VFA in the first sample taken from the ceca of rock ptarmigan in interior Alaska

Month	Sample size	Molar percentage of VFA		
		Acetate	Propionate	Butyrate
April	8	71.0(9.4)*	20.2(8.0)$^{2,3+}$	8.4(1.9)^{2}
July	5	73.8(3.6)	19.9(1.6)^{2,3}	6.2(2.9)^{2,3}
August	9	69.4(2.6)	26.6(3.0)^{1}	4.5(1.4)^{3}
Sept.-Oct.	6	65.7(3.9)	23.6(4.2)^{1,2}	10.7(1.6)^{1}
Nov.-Dec.	7	72.6(2.9)	16.6(2.8)^{3}	10.8(2.0)^{1}
Overall Mean		70.4(5.7)	21.5(5.7)	8.0(3.2)

*Mean (standard deviation).

+Within the same column, values with the same superscript are not significantly different ($P>0.05$); values with different superscripts are significantly different ($P<0.05$). Columns without superscripts have no significantly different values.

TABLE 4. Production rate of VFA in ceca of rock ptarmigan collected in interior Alaska

Month	Sample size	Production rate (μM/g wet contents·min) [% of total] Acetate	Propionate	Butyrate	Total	Initial conc. (μM/g)
April	7	1.00(0.43)* [62]	0.38(0.17)[2,3]+ [24]	0.20(0.10) [13]	1.59(0.42)[1]	24.3(10.9)
July	3	2.3(0.86) [64]	0.99(0.37)[1] [28]	0.29(0.09) [8]	3.58(1.09)[2]	42.3(22.9)
August	9	1.30(0.65) [60]	0.65(0.24)[1,2] [30]	0.22(0.09) [10]	2.15(0.95)[1]	20.8(15.9)
Sept.-Oct.	6	1.17(0.33) [64]	0.41(0.30)[2,3] [23]	0.24(0.19) [13]		
	13				1.93(0.50)[1]	26.5(15.4)
Nov.-Dec.	6	1.37(0.69) [64]	0.43(0.20)[2,3] [20]	0.35(0.09) [16]	2.12(0.88)[1]	27.4(18.0)

*Mean (standard deviation).
[% of total]

+Within the same column, values with the same superscript are not significantly different ($P>0.05$); values with different superscripts are significantly different ($P<0.05$). Columns without superscripts have no significantly different values.

all seasons sampled and the overall mean production was 1.3, 0.53 and 0.25 μM/g•min, respectively. The highest rates of VFA production were found during July, 3.6 μM/g•min ($P<0.05$), whereas production in all other seasons was not significantly different, 1.6 to 2.2 μM/g•min. Production of individual VFA as a per cent of the total production (Table 4) shows the greatest proportion of propionate compared to acetate was produced by birds feeding on green vegetation during summer and early fall. Butyrate during this period was at its lowest proportional production. Thus the pattern of VFA production suggests material entering the cecum during summer probably contained the highest proportion of soluble carbohydrates.

Acetate production as a per cent of total production (Table 4) was less than the proportion occurring in the first cecal sample (Table 3) during all collection periods while the per cent of propionate and butyrate produced were greater than the molar per cent in the first sample of cecal contents. Therefore, differential absorption rates of VFA from the cecum existed and these data indicate relative absorption rates were the following: butyrate>propionate>acetate.

Mean daily production of VFA, calculated from cecal fill and production rates (Table 4) is shown in Table 5 for all collection periods. For purposes of calculation only, the assumption was made that individual birds maintained both cecal fill and VFA production at a constant level for 24 hours. Total average VFA production was high during November-December and July, 34 and 30 mM/day, respectively, although not significantly different from other periods. The general

pattern of VFA production and ME of VFA shows acetate>propionate>butyrate for all seasons. The average ME of VFA during all collection periods was 7.1 kcal/day and seasonal estimates ranged from 5.7 during April to 10.0 during November-December but were not significantly different. The large standard deviations of these values indicates the wide variability found among birds (Table 5). The caloric value of VFA produced as a fraction of the standard metabolic rate did not vary significantly among seasons and averaged 17.5% for all seasons combined.

DISCUSSION

Food selected varied in species composition with season but generally followed the pattern described by Weeden (1969). If these ptarmigan selected the highest quality food which are seasonally available, as found by Moss (1967, 1968) and Gardarsson & Moss (1970), summer foods were of higher nutritional quality than winter foods when based on the chemical analysis used in the present study. Summer and early fall foods consisted of seed and leaves high in protein and cell walls with a low proportion of lignin which suggests they are more digestible than the buds and catkins consumed from September through April which contained low crude protein and highly lignified cell walls (Fig. 1, Table 1). Higher digestibility of foods during summer and early fall should result in decreased DM entering the hindgut and probably the cecum. This may account for the low values of cecal

TABLE 5. Mean daily production of VFA and their equivalent metabolizable energy in ceca of rock ptarmigan collected in interior Alaska

Month	Sample size	Daily production: Acetate mM	Acetate kcal	Propionate mM	Propionate kcal	Butyrate mM	Butyrate kcal	Total mM*	Total kcal	% of standard metabolic rate+
April	7	12.5(4.4)°	2.6(0.9)	4.9(2.5)	1.8(0.9)	2.5(1.0)[1#]	1.3(0.5)[1]	20.0(2.7)	5.7(0.8)	14.7(2.4)
July	3	19.1(5.3)	4.0(1.1)	8.3(1.3)	3.0(0.5)	2.5(0.8)[1]	1.3(0.4)[1]	30.2(4.6)	8.4(1.1)	19.5(2.5)
August	9	13.1(5.9)	2.8(1.2)	6.5(1.7)	2.4(0.6)	2.2(0.8)[1]	1.2(0.4)[1]	21.7(7.1)	6.3(1.9)	15.9(4.6)
Sept.-Oct.	6	13.8(1.9)	2.9(0.4)	4.9(3.0)	1.8(1.1)	2.7(1.8)[1]	1.4(1.0)[1]		6.7(2.7)	
	13							23.0(8.3)		16.7(5.9)
Nov.-Dec.	6	22.1(14.3)	4.6(3.0)	6.9(4.2)	2.5(1.5)	5.4(1.9)[2]	2.8(1.0)[2]	34.0(19.1)	10.0(5.1)	23.5(12.1)
Overall Mean		15.4(8.0)	3.2(1.7)	6.1(2.8)	2.2(1.0)	3.0(1.7)	1.6(0.9)	24.5(10.4)	7.1(3.0)	17.5(6.8)

*Total mM was calculated from the slope of total concentration vs. time rather than the sum of individual acid production.

+Standard metabolism calculated as described by Lasiewski and Dawson (1967), Log M = Log 78.3 + 0.723 Log W where M = kcal/bird/day and W = body weight in kg.

°Mean (standard deviation).

#Within the same column values with the same superscript are not significantly different ($P>0.05$); values with different superscripts are significantly different ($P<0.05$). Columns without superscripts have no significantly different values.

fill observed during this period and in captive ptarmigan which were maintained on a high plane of nutrition (Moss 1972; Gasaway et al., 1975a). The cecum may compensate for this reduction in DM input by decreasing length, diameter and tissue weight during spring and summer while during fall and winter gradually increasing in size in response to greater DM flow (Fig. 2). The cellular changes associated with the cecum's annual two-fold weight fluctuation and 15 cm length change are unstudied.

The food with a high probability of entering the cecum is soluble or suspended fine particles which have escaped digestion and absorption in the upper gut (Gasaway et al., 1975a, 1975b). The nutritional quality of this DM entering the cecum may be indicated seasonally by the rate at which it is fermented in the cecum. Thus the significantly high fermentation rate during July suggests DM of greater quality was entering the cecum during this period than other seasons of the year. The low ratio of acetate/propionate production during summer also supports this concept since high quality substrates generally result in lower acetate/propionate ratios when fermented by rumen bacteria (Hungate, 1966) and possibly in cecal fermentation systems also.

Food consumed during August was of as high quality as in July, however the only data that suggested DM entering the cecum during August was of higher quality than that entering during winter was the low ratio of acetate to propionate (Table 3 and 4). Thus the quality of the food selected may not directly reflect the composition of DM entering the cecum since cecal DM must have first undergone partial

digestion in the upper GI tract. However, the July sample on which this tentative conclusion is partially based was small due to a loss of samples from several birds, hence less confidence is placed in the July values.

The pattern of individual VFA production in the rock ptarmigan ceca was similar to that found in willow ptarmigan, i.e. acetate> propionate>butyrate (Gasaway, 1975). However, the proportions of each acid varied considerably between the two species of ptarmigan. Cecal microbes of willow ptarmigan produced relatively greater proportions of butyrate and propionate and less acetate than in ceca of rock ptarmigan (Gasaway, 1975). These differences are probably due to the chemical makeup of DM entering the cecum and/or varying microbial species in the ceca of rock and willow ptarmigan.

From the difference between the per cent of acetate, propionate and butyrate produced and the per cent present in cecal contents, it was concluded that the relative absorption rates were as follows: butyrate>propionate>acetate. This same pattern of absorption has been reported in willow ptarmigan (Gasaway, 1975) and in cecum of sheep (Myers et al., 1967), and Hoover & Heitmann (1972) reported propionate and butyrate to be absorbed faster than acetate in rabbits. However, conflicting data from in vivo experiments with chickens and ducks indicated that propionate was absorbed significantly faster than acetate or butyrate from the cecum (Barza, 1966; Parhon & Barza, 1967). They reported absorption to increase as concentration of the VFA increased. However, in present studies butyrate was absorbed at the

greatest rate yet was present in the lowest concentration in cecal contents. In vitro experiments show very little VFA is metabolized by the cecum of the fowl suggesting most VFA are absorbed in the blood and transported to other organs where they are oxidized (Parhon & Barza, 1967). Essentially all VFA produced in the cecum of rock ptarmigan were absorbed since it was calculated that only 2% of the VFA produced was excreted in cecal droppings.

Estimates of ME available to rock ptarmigan from cecal VFA production exceeded ME available to the larger willow ptarmigan, 7.1 and 5.7 kcal/day, respectively, which were equal to 17.5% and 11% of the standard metabolic rate for rock and willow ptarmigan, respectively (Gasaway, 1975; Lasiewski & Dawson, 1967). However, West (1972) reports resting metabolic rates of rock ptarmigan during winter to be about 71 kcal/day which is about 160% of standard metabolism calculated by the equation of Lasiewski & Dawson (1967). Using West's estimate, cecal fermentation would supply approximately 10% of resting metabolic requirements.

The free living energy requirement of wild rock ptarmigan during winter was estimated to be 100 kcal ME (Moss, 1973) and if energy requirements are assumed to be equal during all seasons, VFA would supply an average 7% of the ME. However, this value is considerably greater than the estimated 3.8% of free living energy supplied by fermentation in willow ptarmigan and the 2.5% of the digestible DM absorption from the cecum of captive rock ptarmigan (Gasaway, 1975; Gasaway et al., 1975b). Approximately 93% of the ME requirements

of wild rock ptarmigan must therefore be supplied by digestion and absorption of nutrients from the stomach and small intestine which is just slightly longer than the combined length of the ceca. Hence, for its relatively larger size, the cecum appears to supply only a small fraction of the total energy needs of rock and willow ptarmigan.

SUMMARY

1. Seasonal changes in the chemical and taxonomic character of the diet, the size of the cecum and cecal volatile fatty acid (VFA) production were studied in rock ptarmigan collected in interior Alaska.

2. Ptarmigan fed predominantly on buds and catkins of dwarf birch from late September through April and consumed a significant proportion of berries when available during this period, while seeds predominated in crop contents during July and leaves were preferred during August.

3. Foods selected during July and August were of higher nutritional quality than those selected during other seasons. Crude protein values were highest and lignification of the cell wall lowest in foods selected by ptarmigan during the plant growing season.

4. The length, weight of contents and tissue weight of the cecum were greatest during winter, declined to their shortest, lightest state during summer and early fall and again increased as winter approached.

5. Relative production rates of individual VFA were acetate>propionate>butyrate, whereas relative absorption rates were butyrate>

propionate>acetate.

6. The proportion of propionate produced with respect to acetate was highest during summer and early fall suggesting material entering the cecum during these seasons contained the highest proportion of soluble carbohydrates.

7. Seasonal VFA fermentation rates/g of cecal contents differed significantly only during July when the rate was highest.

8. Total VFA production/day did not differ significantly among seasons and metabolizable energy available from VFA averaged 7.1 kcal/day. This energy was equivalent to about 18% of the standard metabolic rate and 7% of estimated free living energy requirements.

REFERENCES

ANNISON E. G., HILL K. J. & KENWORTHY R. (1968) Volatile fatty acids in the digestive tract of the fowl. Br. J. Nutr. 22, 207-216.

BARZA E. (1966) Absorbtia cizilor grosi volatili in cecumuri, La pasari. Lucrarile Stiintifice ale Institulalui Agronomicn Balcescu Bucuresti, Series C 9, 583-589.

CARROLL E. J. & HUNGATE R. E. (1954) The magnitude of microbial fermentation in the bovine rumen. Appl. Microbiol. 2, 2505-2514.

GARDARSSON A. & MOSS R. (1970) Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. In: Animal Populations in Relation to Their Food Resources. (Edited by Watson A.), pp. 47-71, Blackwell Scientific Publications, Oxford and Edinburgh.

GASAWAY W. (1975) Volatile fatty acid production and metabolizable energy derived from cecal fermentation in willow ptarmigan. In prep.

GASAWAY W., HOLLEMAN D. & WHITE R. (1975a) Digesta flow in the intestine and cecum of the rock ptarmigan. In prep.

GASAWAY W., WHITE R. & HOLLEMAN D. (1975b) Dry matter digestion and water absorption in the intestine and cecum of rock ptarmigan. In prep.

GOERING H. R. & VAN SOEST P. J. (1970) Forage fiber analysis (apparatus, reagents, procedures and some applications). Agriculture Handbook No. 379, Jacket No. 387-598, USDA.

GRAY T. C. & STEVENS B. J. (1966) Analysis of the lower free fatty acids from microbial fermentation. Analyt. Chem. 38, 724-726.

HAWK P. B., OSER B. L. & SUMMERSON W. H. (1947) Practical Physiological Chemistry. 13 edition. The Blankiston Co., Inc., New York. p. 1439.

HODGMAN C. D., WEAST R. C. & SELBY S. M. [eds.]. (1958) Handbook of Chemistry and Physics. 39 edition. Chemical Rubber Publishing Co., Cleveland, Ohio. p. 3213.

HOOVER W. H. & HEITMANN R. N. (1972) Effects of dietary fiber levels on weight gain, cecal volume and volatile fatty acid production in rabbits. J. Nutr. 102, 375-380.

HUNGATE R. E. (1966) The rumen and its microbes. Academic Press, New York. p. 533.

IRVING L., WEST G. & PEYTON L. (1967) Winter feeding program of Alaska willow ptarmigan shown by crop contents. Condor 69, 69-77.

LASIEWSKI R. & DAWSON W. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69, 13-23.

LEOPOLD A. S. (1953) Intestinal morphology of gallinaceous birds in relation to food habits. J. Wildl. Mgmt. 17, 197-203.

MCBEE R. H. & WEST G. C. (1969) Cecal fermentation in the willow ptarmigan. Condor 71, 54-58.

MOSS R. (1967) Probable limiting nutrients in the main food of red grouse (Lagopus lagopus scoticus). In: Secondary Productivity of Terrestrial Ecosystems. (Edited by Petrusewicz K.), pp. 369-379, Vol. I, PWN-Polish Scientific Publishers, Warszawa and Krakow.

MOSS R. (1968) Food selection and nutrition in ptarmigan (Lagopus mutus). In: Comparative Nutrition of Wild Animals (Edited by Crawford M. A.), pp. 207-216, Academic Press, London.

MOSS R. (1972) Effects of captivity on gut lengths in red grouse. J. Wildl. Mgmt. 36, 99-104.

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

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

MYERS L. L., JACKSON H. D. & PACKETT L. V. (1967) Absorption of volatile fatty acids from the cecum of sheep. J. An. Sci. 26, 1450-1458.

PARHON C. C. & BARZA E. (1967) Recherches sur l'absorption caecale chez les oiseaux domestiques. Rev. Roum. Biol.-Zoologie 12, 109-115.

STEEL R. & TORRIE J. (1960) Principles and procedures of Statistics. McGraw-Hill Book Co. Inc., New York. p. 481.

WEEDEN R. B. (1961) Outer primaries as indicators of age among rock ptarmigan. J. Wildl. Mgmt. 25, 337-339.

WEEDEN R. B. (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86, 271-281.

WEST G. C. (1972) Seasonal differences in resting metabolic rate of Alaskan ptarmigan. Comp. Biochem. Physiol. 42, 867-876.

CHAPTER IV.

VOLATILE FATTY ACIDS AND METABOLIZABLE ENERGY DERIVED FROM CECAL FERMENTATION IN THE WILLOW PTARMIGAN

INTRODUCTION

Seasonal variation in food selection, cecum size, fermentation rates in the cecum and metabolizable energy attained from fermentation products in rock ptarmigan, Lagopus mutus, have been described by Gasaway (1975). The ecological requirements and food habits of willow ptarmigan, Lagopus lagopus, differ from those of rock ptarmigan (West & Meng, 1966; Weeden, 1969). For this reason an interspecific comparison of cecal functions in rock and willow ptarmigan was undertaken. Numbers and types of bacteria found in cecal contents and cecal fermentation rates have been previously reported for willow ptarmigan by McBee & West (1969). The present report further describes volatile fatty acids (VFA) production in the cecum and the contribution made by VFA metabolizable energy (ME) to total metabolic energy requirements of willow ptarmigan during winter and compares them with rock ptarmigan.

MATERIALS AND METHODS

Willow ptarmigan were collected in the Alaska Range along the Richardson Highway from mile 200 to 215 (65°30' N lat.; 145°25' W long.) during April 1970. Fourteen individual birds were shot and immediately taken to a warm vehicle where the body weight was recorded and the cecum was removed, weighed with contents and length measured. The cecum was then opened and contents transferred to a glass vial,

incubated, periodically sampled and specimens preserved as described by Gasaway (1975). Cecal tissue was weighed after contents were removed. Sex of birds was noted and the crop contents were removed and stored for chemical and taxonomic analysis. The total time required to complete the sampling of 1 bird was approximately 30 minutes.

Preserved cecal contents were later analyzed for concentrations and composition of VFA. Cecal contents of these birds were determined by the sum of all sample weights.

An additional 21 willow ptarmigan were collected in the same study area to provide a larger sample for physical measurements of cecum size. Body weights, ceca length and weight including contents were determined. Crop contents were removed and stored for chemical and taxonomic analysis.

Dietary nutrients (crude protein, neutral detergent fiber (NDF), acid detergent fiber (ADF), lignin, cellulose and lipids) were analyzed (Gasaway, 1975).

Proceedures for in vitro incubation of cecal contents, qualitative steam distillation of VFA and qualitative analysis of VFA by gas liquid chromotography were described by Gasaway (1975). VFA production for acetic, propionic, butyric and total acids (μM/g$\cdot$min) was determined by the "zero time" method from the slope of the regression line of VFA concentration (μM/g fresh contents) versus time in minute after death (Carroll & Hungate, 1954; Gasaway, 1975). Production of acetic, propionic butyric and total acids (μM/g fresh contents$\cdot$min) were

calculated for each bird. Initial concentration of VFA (μM/g fresh contents) in cecal contents at time of death was estimated by the y intercept of the total VFA production regression line.

The production of VFA/bird (mM/bird•min) was calculated by multiplying the mM/g•min times g cecal fill. Extrapolation of VFA production for a 24 hour period (mM/bird•day) was calculated by multiplying mM/bird•min times min/day.

Metabolizable energy (ME) of VFA is equal to the caloric value of its heat of combustion, i.e. acetate, propionate and butyrate equal 209.4, 367.2 and 524.3 kcal/mole, respectively (Hodgman et al., 1958). Therefore, the ME of VFA produced in the cecum/day was equal to moles of VFA produced times its respective caloric value.

RESULTS

Taxonomic and chemical analysis of food

Willow (Salix) comprised 93% of the crop contents of which 64.7% were twigs and 28.5% were buds (Table 1). Birch (Betula) buds and catkins and aspen (Populus tremuloides) buds and twigs represented 5.6 and 1.3% of the crop contents (Table 1).

Crude protein was higher in buds and catkins of all species compared with woody twigs, while willow buds contained the highest proportion of crude protein (Table 1).

All samples contained large amounts of cell contents, with

Table 1--Per cent chemical composition of crop contents from 35 willow ptarmigan collected in the Alaska Range, Alaska, April 1971

Plant	% of diet	Crude protein	Cell contents	Neutral detergent fiber (NDF)	Acid detergent fiber (ADF)	Lignin	Lignin ADF	Cellulose	Lipid
Salix (twigs)	64.7	9.4	62.2	37.8	34.7	20.0	0.58	14.6	9.4
Salix (buds)	28.5	14.8	61.4	38.6	35.7	15.5	0.43	20.2	3.8
Betula (buds)	1.8	13.3	75.1	24.9	21.6	14.6	0.68	7.0	18.6
Betula (catkins)	3.8	13.1	76.1	23.9	28.8	20.4	0.71	8.4	8.2
Populus (buds)	0.6	12.2	78.4	21.4	20.5	12.4	0.61	8.0	20.2
Populus (twigs)	0.7	9.5	--	--	--	--	--	--	--
Total diet	100.1	11.2	63.0	37.0	34.3	18.5	0.55	15.8	7.5

significantly higher levels in Betula and Populus than in Salix (Table 1); in comparison the ADF component was highest in Salix. The degree of lignification in ADF is indicated by the lignin/ADF ratio (Table 1). The fiber component of all plant parts was highly lignified, but Salix buds and twigs contained the lowest proportion of lignin in ADF of all dietary components. Cellulose was inversely related to lignin in fiber, hence Salix contained the highest proportion of cellulose, the most digestible portion of the ADF. Buds of Betula and Populus contained significantly higher ether extractable fractions than other plant parts.

The chemical composition of the total diet was similar to the composition of Salix buds and twigs due to their high proportion in the diet.

Physical characteristics of the cecum

The combined length of both ceca averaged 100 cm in females and 107 cm in males (Table 2). Average cecal fill for birds during the 11 hour sample period was 7.7 g (Table 2) with a range of 2.8 to 14.7 g. Cecal contents were 1.3 and 1.2% of body weight for females and males, respectively. The weight of the cecum with contents averaged 29 and 32 g fresh weight in females and males, respectively, while the per cent of live weight was 5.5 and 5.3% (range 3.9-7.6%) for females and males, respectively.

Ceca were generally emptied by 0900 hours and the ceca filled during the day reaching their greatest volume near sunset (Fig. 1). A few birds emptied their ceca about 1800 hours possibly for the second time that

Table 2--Cecum length, weight, fill and proportion of body weight in willow ptarmigan collected during April 1971 in interior Alaska.

Sex	Combined length of ceca (cm)	Cecum[++] contents (g)	Estimated[S] weight of cecum contents (g)	Fresh tissue weight of cecum (g)	Total ceca wt (g)	Body wt (g)	Cecum conents (% of body wt)	Total cecum wt (% of body wt)
Female	100(10)* n=5[+]	7.6(2.9) n=7	6(2) n=8	23(1) n=4	29(2) n=8	502(38) n=16	1.3(0.5) n=15	5.5(0.8) n=15
Male	107(8) n=18	7.8(3.4) n=9	7(4) n=10	25(1) n=6	32(5) n=10	587(48) n=18	1.2(0.6) n=18	5.3(1.0) n=18
Combined	104(10)	7.69(3.1)	6(4)	24(1)	31(4)	548(62)	1.2(0.6)	5.4(0.9)

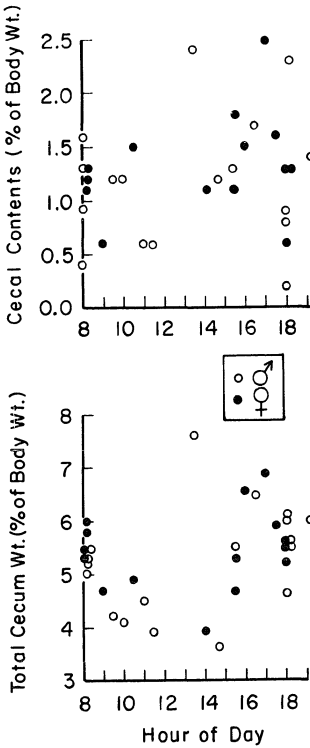
*Mean (standard deviation).

[+]n=sample size.

[++]Actual weight of contents.

[S]Estimated weight of ceca = total ceca weight - mean tissue weight of cecum.

Fig. 1. Cecal contents and total cecum weight (organ + contents) as a per cent of body weight during daylight hours in willow ptarmigan collected during April 1971 in interior Alaska (●, female; ○, male).



day. Cecal fill at night is unknown due to the difficulties of collecting birds after dark.

VFA production

Molar proportions of VFA in the cecum of willow ptarmigan at the time of death were approximately the same as molar proportions in the first sample taken from the cecum. Average molar percentages of acetate, propionate, butyrate and valerate were 63.7, 22.7, 12.4 and 0.3%, respectively (Table 3). Acids formed from protein fermentation, e.g. isobutyrate and isovalerate (Hungate, 1966), were found in trace amounts, suggesting very little protein may have been fermented. Molar proportions changed in the cecal contents during in vitro incubation due to differential production rates of each acid. Therefore, molar proportions of VFA in each subsample had to be determined for production rate studies.

Production of acetate, propionate and butyrate in whole cecal contents (μM/g·min) are shown in Table 4. Isobutryate, valerate and isovalerate production were not determined since they were present only in trace amounts. No consistent pattern of VFA production was found among individual birds, however, on the average acetate was produced in the greatest quantities followed by propionate and butyrate, 0.66, 0.47 and 0.36 μM/g·min, respectively. Total VFA production, estimated from the concentration of all acids, averaged 1.51 μM/g·min.

Forty-four per cent of VFA produced was acetate (Table 4) and this proportion was less than the proportion occurring in the first cecal sample, 64%, (Table 3) while the percentages of propionate and butyrate

Table 3--Molar percentage of VFA in the first sample taken from the ceca of 14 willow ptarmigan during April 1971 in interior Alaska

Acetate	Priopionate	Butyrate	Isobutyrate	Valerate	Isovalerate
63.7(8.8)*	22.7(3.3)	12.4(8.1)	0.4(0.2)	0.3(0.1)	0.4(0.2)

*Mean (standard deviation).

Table 4--Production rate of VFA in ceca of 14 willow ptarmigan collected in interior Alaska during April 1971

Production rate (μ moles/g wet contents·min)				Initial Concentration (μM/g)	Cecum contents (g)
Acetate	Propionate	Butyrate	Total		
0.85	0.27	0.30	1.40	16.0	7.3
-0.30	0.44	0.76	0.94	15.0	7.2
0.20	0.30	0.40	0.90	16.4	7.5
0.90	0.90	0.40	2.20	27.3	3.2
--	--	--	1.73	26.5	3.4
0.49	0.46	0.11	1.05	22.9	14.7
0.61	0.93	0.40	1.90	21.2	6.3
1.06	0.52	0.40	2.01	13.9	8.2
1.06	0.72	0.16	1.94	15.0	8.7
0.72	0.35	0.16	1.22	27.7	9.2
0.82	0.38	0.38	1.60	8.8	12.4
1.00	0.30	0.10	1.50	23.8	8.6
0.49	0.19	0.54	1.20	21.1	9.5
0.71	0.34	0.51	1.50	16.0	7.5
0.66(0.38)*	0.47(0.24)	0.36(0.19)	1.51(0.41)	19.4(5.77)	
% of total production	44	32	24		

*Mean (standard deviation).

produced were greater than the molar percentages in the first sample. These data suggest either a differential absorption pattern of VFA; the longer chained acids being absorbed more readily than acetate or that there is a conversion of acetate to longer chain acids in vitro.

On a daily basis total production of VFA in the ceca of willow ptarmigan averaged 16.85 mM/bird for ptarmigan in all stages of cecal fill (Table 5), however, the range of production varied about three fold, 8.5 to 28.6 mM/bird/day. The pattern of VFA production shows acetate was produced in greatest quantities followed by propionate and then butyrate, 7.92, 5.12 and 3.83 mM/bird/day. However, butyrate production yielded the greatest ME followed by propionate and acetate, 2.08, 1.88 and 1.70 kcal/bird·day, respectively (Table 5). The average ME available/day from VFA was 5.66 kcal ranging among individual birds from 2.26 to 9.12 kcal. Butyrate production was exceptionally high in several birds and in the bird with the highest butyrate production, acetate had an apparent negative production rate (Table 5).

DISCUSSION

Willow ptarmigan during winter feed primarily on willow buds and twigs in Alaska (West & Meng, 1966; Weeden, 1969), but the proportion of twigs to buds consumed is probably dependent on the availability of buds. Birds collected during late winter for this study had selected a relatively large proportion of twigs (64.7%) relative to buds (28.5%).

Table 5--Mean daily production of VFA and its equivalent available metabolizable energy in ceca of 14 willow ptarmigan shot during April in interior Alaska

Daily production							
Acetate		Propionate		Butyrate		Total	
mM	kcal	mM	kcal	mM	kcal	mM*	kcal
7.92(4.82)+	1.70(0.91)	5.12(2.51)	1.88(0.92)	3.83(2.37)	2.08(1.40)	16.85(6.11)	5.66(1.83)

*Total mMoles was calculated from the slope of total concentration vs time rather than the sum of individual acid production.

+Mean (standard deviation).

The selection of willow twigs may be due in part to repeated browsing of willows by ptarmigan during winter which may have reduced the proportion of buds available in relation to twigs. Moss (1967, 1968) and Gardarsson & Moss (1970) have shown that red grouse, Lagopus lagopus scoticus, and rock ptarmigan do select the most nutritious foods available. A greater proportion of crude protein, a lesser degree of lignification and equal proportion of cell contents of buds with respect to twigs suggests willow buds should be more nutritious than twigs, although the outer layers of the twig which are ground off in the gizzard and digested may be of higher nutritional value than is indicated by data from the entire twig. Cecal digestion and fermentation of the fibrous component of the diet would be greatest in the least lignified foods (Van Soest, 1964), thus as judged from the lignin/ADF ratio, the fibrous component of Salix twigs and buds is relatively more nutritious than the other dietary components, Betula and Populus twigs, buds and catkins (Table 2).

Willow ptarmigan appeared to empty their ceca in early morning and fill during the day (Fig. 1). The emptying schedule is unknown in wild willow ptarmigan although G. West (pers. comm.) indicated captive willow ptarmigan feeding on commercial rations emptied the cecum once a day. On the other hand, captive rock ptarmigan, also feeding on commercial feed, empty their ceca 2 to 3.2 times per day (Gasaway et al., 1975a, 1975b). If the cecum empties once per 24 hours and filling is continuous between cecal defecations, as in rock ptarmigan (Gasaway et al., 1975a), filling would continue into the night. However, if the cecum empties twice daily, it probably empties near the end of the day and in the early

morning as suggested by low cecal fill in some individuals during these periods (Fig. 1). And it is highly probable that many birds do not reach maximum fill before emptying their ceca which would appear inefficient. Wide variability in cecal fill at the time of emptying and after emptying was reported in captive rock ptarmigan by Gasaway et al. (1975a) which may explain the wide range of cecal fills early in the day in willow ptarmigan which appeared to have recently emptied their ceca.

The pattern of molar concentration of VFA found in cecal content of willow ptarmigan, i.e. acetate>propionate>butyrate, confirms that reported by McBee & West (1969) and was characteristic of that found in rock ptarmigan (Gasaway, 1975), red grouse (Moss, 1973), domestic fowl (Annison et al., 1968), horse (Hintz et al., 1971), pig (Farrell & Johnson, 1970), kangaroo, Macropus gigantus, Megaleia rufa, guinea pig (Henning & Hird, 1970) and in wild and domestic ruminants (Gasaway & Coady, 1974). However, a number of studies have shown equal or higher concentrations of butyrate than propionate in cecal contents of the white rat (Yang et al., 1969), wild rabbit, Oryctolagus cuniculus, (Henning & Hird, 1972), rabbit (Hoover & Heitmann, 1972), beaver, Castor canadensis, (Hoover & Clarke, 1972) and the porcupine, Ereithiezon dorsatum, (Johnson & McBee, 1967). Therefore the pattern of VFA production is not similar in all fermentation systems. Rumen microbes generally produce the highest proportions of propionate when the host diet is high in soluble carbohydrate (Hungate, 1966). However, digesta entering the cecum has had a large portion of the digestible soluble carbohydrate removed in

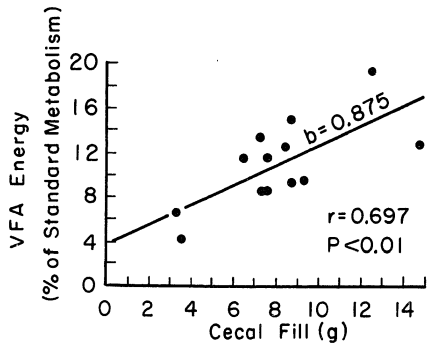
the foregut. Hence, the high proportion of butyrate in relation to propionate found in the cecum of the willow ptarmigan and other species may be due to a lower proportion of soluble carbohydrate entering the cecum.

The average molar percentages of VFA in the first sample as opposed to subsequent samples of cecal contents were greater for acetate and less for propionate and butyrate than the per cent of each acid produced in vitro which suggests VFA were not absorbed in the same ratio as they were produced (Table 3 and 4) or possibly that there is a considerable conversion of acetate to propionate and butyrate in vitro (Leng & Leonard, 1965). Based on these data, the relative indicated rates of absorption of acids from the cecum of willow ptarmigan were butyrate>propionate>acetate, and this trend is similar to the absorption pattern reported for the cecum of domestic sheep (Myers et al., 1967). Hoover & Heitmann (1972) reported butyrate and propionate to be absorbed faster than acetate in rabbits and data presented by Johnson & McBee (1967) indicate a similar, though less pronounced, absorption pattern in the porcupine.

In spite of a general decline in fermentation rate with increasing fill, total fermentation and energy yield per bird increased with cecal fill in willow ptarmigan (Fig. 2), whereas in rock ptarmigan, total fermentation was generally similar at all stages of fill (Gasaway, 1975) due to a greater decline in fermentation rates as fill increased. Therefore, in willow ptarmigan the least amount of ME is supplied following a cecal defecation and increases as the cecum refills.

Rates of cecal VFA production determined in the present study were

Fig. 2. The correlation between VFA energy produced in the cecum as precentages of standard metabolic rate with grams cecal fill in willow ptarmigan collected during April 1971 in interior Alaska.



generally higher than those reported for willow ptarmigan by McBee & West (1969). McBee & West, as in the present report, found highly variable production rates for acetate, propionate and butyrate, however in 5 out of 8 birds they found no net production of 1 or 2 VFA. The *in vitro* incubation and sampling methods used by McBee & West (1969) were dependent on uniform mixing of cecal contents since they sampled the cecum contents by cutting it into 3 nearly equal lengths. My observations on cecal fill in willow ptarmigan indicate uniform mixing probably does not occur for a significant portion of the time. The ME from VFA in the present study averaged 5.7 kcal/day and ranged from 2.3 to 9.1 kcal (Table 5) due to varying production rates and produced 5.7 kcal ME/day of VFA and all other birds were significantly lower when an average of 10 g cecal fill is used to calculate VFA production. However, McBee & West (1969) reported ethanol production in 3 of 8 birds. In one individual, ME resulting from ethanol production was nearly equal to VFA energy. Unfortunately no estimates of ethanol production were made in the present study and hence the present estimates of energy dervied from the cecum may be minimal as ethanol may at times be an important end product of cecal fermentation in ptarmigan.

Cecal fermentation appears to provide only a small portion of the total energy required by willow ptarmigan. The average fraction of standard metabolism (Lasiewski & Dawson, 1967) supplied by fermentation was 11% while the proportion of energy obtained from fermentation was even less when compared with existence and free living energy requirements (Table 6). West (1968) has shown willow ptarmigan caged outdoors during

Table 6--The per cent of energy requirements supplied by VFA in willow ptarmigan in interior Alaska

Average body wt (g)		Standard* metabolism	Existence+ at 30°C	Existence++ during winter in Alaska	Free living^{S} during winter in Alaska
559°	Energy Requirements	51.4	63.9	119	150
	% energy supplied by VFA	11.0(4.3-19.4)°°	8.9(3.5-14.3)	4.8(1.9-7.7)	3.8(1.5-6.1)

*Lasiewski and Dawson (1967), log M = log 78.3 + 0.723 log body weight in kg.

+Kendeigh (1970), log M = -0.2673 + 0.7545 log body weight in g where M = kcal/bird per 24 hr.

++West (1968), measured in caged birds held outdoors during winter.

^{S}Moss (1973), estimated for free living willow ptarmigan in the same area as the present study.

°Weight of the 13 birds which were used in the VFA production measurements.

°°Range of values.

winter required 119 kcal/day whereas free living wild willow ptarmigan require 150 kcal ME/day during winter (Moss, 1973). Thus cecal fermentation provided only 4.8 and 3.8% of existence and free living energy needs, respectively.

However, energy derived from cecal fermentation increased as the cecum filled between cecal defecations and reached a maximum at the time of emptying (Fig. 2). Therefore, during a portion of the day ME from fermentation may be as high as twice and as low as half the mean values in an individual bird.

Limited data suggests the avian cecum is more efficient than ceca of mammalian species. Cecal contents expressed as a per cent of body weight for mammalian herbivores were greater than for the avian species with the possible exception of the pig (Table 7). Mammals also divert a higher proportion of the total digesta into the cecum whereas birds separate digesta into two fractions, diverting the more digestible fraction to the cecum (Gasaway et al., 1975a, 1975b) and defecating the non-digestible material. Thus the net result is a relatively higher porportion of the standard metabolic rate supplied from avian cecal fermentation by a smaller organ when compared to mammals. The evolution of this small but highly efficient cecum is compatible with the general evolutionary trend in birds of a lightweight, streamlined body form in comparison with the mammalian body form. Optimum cecum size in avian herbivores probably is an evolutionary compromise between nutritional benefits including energy obtained from oxidation of substrates, and the detrimental effects of increasing

Table 7--The contents of the cecum as per cent of body weight, VFA production rates per g whole contents and energy derived from VFA as per cent of basal metabolic rates in various mammalian and avian herbivores

Species	Contents (% of body wt)	VFA production (μM/g whole contents·hr)	Energy (% of basal rate)	Reference
Rabbit	7.8			Elsden et al. (1946)
Porcupine	4.4	27	16	Johnson & McBee (1967)
Beaver	2.1			Hoover & Clark (1972)
Horse	2.5			Elsden et al. (1946)
Rabbit	1.8-2.5	41	10-12	Hoover & Heitmann (1972)
Rat	1.8-2.4		9.4	Yang et al. (1969, 1970)
Rock ptarmigan	2.1	138	18	Gasaway (1975)
Sharp-tailed grouse	1.4	126	14	Gasaway (unpub. data)
Willow ptarmigan	1.2	91	11	Present study
Pig	0.4-0.7	50	5.8	Farrell & Johnson (1970)

cecum weight and volume on mobility and balance.

Approximately 4% of the free living energy requirements of ptarmigan was supplied by the cecal fermentation, but the actual nutritional value derived from the cecum is likely to be greater if size of the cecum with respect to the total gut is any indication. The combined length of ceca were nearly equal to the entire gut length. The cecum and its contents averaged 5.4% of the total body weight in willow ptarmigan and reached as much as 7.6%. This small fraction of total energy requirement supplied by fermentation could possibly be met by greater food consumption and increased digesta volume and flow rates, since monogastric cecal fermentors, unlike ruminants, have the capability of increasing digesta flow rates and food consumption when food quality decreases resulting in a net gain of ME (Bell, 1971). Therefore, if fermentation is the major function of the cecum, the present study and others by McBee & West (1969) and Gasaway (1975) have possibly underestimated the contribution of the cecum in the nutrition of ptarmigan. Underestimates of cecal function may arise from techniques which do not reproduce in situ fermentation. For example, Whitelaw et al. (1970) suggest that estimates of VFA production in the rumen may be considerably underestimated by the in vitro techniques in comparison with in vivo techniques using radioisotopic techniques. Also, the fermentation products produced in vitro may represent only a portion of the dry matter absorbed from the cecum. Functions of the cecum other than energy production may justify the size of the organ. Vitamin synthesis (Coates & Jayne-Williams, 1966; Jayne-Williams & Fuller, 1971), water and electrolyte absorption

(Gasaway et al., 1975b; Parham & Barza, 1967), synthesis and absorption of essential amino acid and other little known functions may make a large cecum essential for successful inhabitance of the niche of avian herbivores.

SUMMARY

1. Volatile fatty acid (VFA) production in the cecum, cecum size and fill, type of food and chemical composition of food were determined for willow ptarmigan shot during April in interior Alaska.

2. Willow buds and twigs comprised 93% of the crop contents; willow buds were the most nutritious item in the crop based on chemical qualities.

3. The cecum averaged 100 and 107 cm in females and males, respectively, and total cecum weight was 5.4% of body weight for both sexes.

4. The average production of acetate, propionate and butyrate was 0.66, 0.47 and 0.36 μM/g·min, respectively, while the relative rates of absorption of these acids were butyrate>propionate>acetate. VFA production for a 24 hour period averaged 16.9 mM which was equivalent to 5.7 kcal metabolizable energy (ME).

5. The per cent of standard metabolism, existence and free living energy requirements supplied by the ME of VFA were estimated to be 11, 4.8 and 3.8%, respectively.

6. A comparison of cecal fermentation rates and cecum size suggested avian species have a more efficient cecum than mammals.

REFERENCES

ANNISON E. G., HILL K. J. & KENWORTHY R. (1968) Volatile fatty acids in the digestive tract of the fowl. Br. J. Nutr. 22, 207-216.

BELL R. H. (1971) A grazing ecosystem in the Serengeti. Sci. Am. 225, 86-93.

CARROLL E. J. & HUNGATE R. E. (1954) The magnitude of the microbial fermentation in the bovine rumen. Appl. Microbiol. 2, 2505-2514.

COATES M. E. & JAYNE-WILLIAMS D. J. (1966) Current views on the role of the gut flora in nutrition of the chicken. In: Physiology of the Domestic Fowl. (Edited by Horton-Smight C. & Amoroso E.), pp. 181-198, Oliver and Boyd, Edinburgh.

ELSDEN S. R., HITCHCOCK M. W., MARSHALL R. A. & PHILLIPSON A. T. (1964) Volatile fatty acid in the digesta of ruminants and other animals. J. Exp. Biol. 22, 191-202.

GARDARSSON A. & MOSS R. (1970) Selection of food by Icelandic ptarmigan in relation to its availability and nutritive value. In: Animal Populations in Relation to Their Food Resources. (Edited by Watson A.), pp. 47-71, Blackwell Scientific Publications, Oxford, England.

GASAWAY W. (1975) Volatile fatty acid production and metabolizable energy derived from cecal fermentation in rock ptarmigan. In prep.

GASAWAY W. & COADY J. (1974) Review of energy requirements and summer function in moose and other ruminants. Proc. of International Symp. on Moose Ecology, Quebec. Le Naturaliste Canadien. In press.

GASAWAY W., HOLLEMAN D. & WHITE R. (1975a) Digesta flow in the intestine and cecum of the rock ptarmigan. In prep.

GASAWAY W., WHITE R. & HOLLEMAN D. (1975b) Dry matter digestion and water absorption in the intestine and cecum of rock ptarmigan. In prep.

FARRELL D. J. & JOHNSON K. A. (1970) Utilization of cellulose by pigs and its effects on caecal function. Anim. Prod. 14, 209-217.

HENNING S. J. & HIRD F. J. (1970) Concentrations and metabolism of volatile fatty acids in the fermentive organs of two species of kangaroo and the guinea pig. Br. J. Nutr. 24, 145-155.

HENNING S. J. & HIRD F. J. (1972) Diurnal variation in the concentrations of volatile fatty acids in the alimentary tracts of wild rabbits. Br. J. Nutr. 27, 57-64.

HINTZ H. F., ARGENZIO R. A. & SCHRYVER H. F. (1971) Digestion coefficients, blood glucose levels and molar percentages of volatile acids in intestinal fluid of ponies fed varying forage grain ratios. J. An. Sci. 33, 992-995.

HODGMAN C. D., WEAST R. C. & SELBY S. M. [eds.] (1958) Handbook of Chemistry and Physics. 39 edition. Chemical Rubber Publishing Co., Cleveland, Ohio. p. 3213.

HOOVER W. H. & CLARK S. D. (1972) Fiber digestion in the beaver. J. Nutr. 102, 9-16.

HOOVER W. H. & HEITMANN R. N. (1972) Effects of dietary fiber levels on weight gain, cecal volume and volatile fatty acid production in rabbits. J. Nutr. 102, 375-380.

HUNGATE R. W. (1966) The rumen and its microbes. Academic Press, New York. p. 533.

JAYNE-WILLIAMS D. J. & FULLER R. (1971) The influence of the intestinal microflora on nutrition. In: Physiology and Biochemistry of the Domestic Fowl. (Edited by Bell D. S. & Freeman B. M.), pp. 73-92, Vol. I, Academic Press, New York.

JOHNSON J. L. & MCBEE R. H. (1967) The porcupine cecal fermentation. J. Nutr. 91, 540-546.

KENDEIGH S. C. (1970) Energy requirements for existance in relation to size of bird. Condor 72, 60-65.

LASIEWSKI R. & DAWSON W. (1967) A re-examination of the relation between standard metabolic rate and body weight in birds. Condor 69, 13-23.

LENG R. A. & LEONARD G. J. (1965) Measurement of the rates of production of acetic, propionic and butyric acids in the rumen of sheep. Br. J. Nutr. 19, 469-484.

MCBEE R. H. & WEST G. C. (1969) Cecal fermentation in the willow ptarmigan. Condor 71, 54-58.

MOSS R. (1967) Probable limiting nutrients in the main food of red grouse (Lagopus lagopus scoticus). In: Secondary Productivity of Terrestrial Ecosystems (Principles and Methods). (Edited by Petrusewicz K.), pp. 369-379, Vol. 1, PWN-Polish Scientific Publishers, Warszawa and Krakow.

MOSS R. (1968) Food selection and nutrition in ptarmigan (Lagopus mutus). Symp. Zool. Soc. Lond. 21, 207-216.

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

MYERS L. L., JACKSON H. D. & PACKETT L. V. (1967) Absorption of volatile fatty acids from the cecum of sheep. J. An. Sci. 26, 1450-1458.

PARHON C. C. & BARZA E. (1967) Recherches sur l'absorption caecale chez les oiseaux domestiques. Rev. Roum. Biol.-Zoologie 12, 109-115.

VAN SOEST P. J. (1964) Symposium on nutrition of forage and pastures: new chemical procedures for evaluating forages. J. An. Sci. 23, 838-845.

WEEDEN R. B. (1969) Foods of rock and willow ptarmigan in central Alaska with comments on interspecific competition. Auk 86, 271-281.

WEST G. C. (1968) Bioenergetics of captive willow ptarmigan under natural conditions. Ecology 49, 1035-1045.

WEST G. C. & MENG M. S. (1966) Nutrition of the willow ptarmigan in northern Alaska. Auk 83, 603-615.

WHITELAW F. G., HYLDGAARD-JENSEN R. S., REID R. S. & KAY M. G. (1970) Volatile fatty acid production in the rumen of cattle given an all-concentrate diet. Br. J. Nutr. 24, 179-195.

YANG M. G., MANOHARAN K. & YOUNG K. (1969) Influence and degradation of dietary cellulose in cecum of rats. J. Nutr. 97, 260-264.

YANG M. G., MANOHARAN K. & MICKELSEN O. (1970) Nutritional contribution of volatile fatty acids from the cecum of rats. J. Nutr. 100, 545-550.

CONCLUSIONS

"The role of the cecum is still something of a mystery" was the conclusion of the most recent review on avian cecal function (McNab, 1973) however, gradually the pieces to the mystery are falling into place. The contribution of the present study represents only a token compared to the full understanding of cecal function. The following summarizes the salient points of this report.

The mechanism by which the cecum of ptarmigan is filled is quite possibly hydrostatic pressure generated from muscular contractions in the intestine. This pressure forces the fluid fraction of digesta which is comprised of water, soluble substances and fine suspended particles through the small opening into the cecum. Species with large ceca and a high rate of turnover of cecal contents, like the rock ptarmigan, divert most of the water entering the hindgut into the cecum where it is absorbed. Thus the cecum becomes the major site for water recovery in these species.

The fluid digesta was continually diverted into the cecum except during periodic cecal discharges which varies in frequency with species, diets and environmental conditions. On the average 55% of the cecal content were evacuated during each discharge. The retained portion of cecal contents probably functions as an innoculum for freshly entered contents containing relatively few bacteria, thus little time lag occurs before maximal bacterial fermentation was achieved following a defecation. Therefore the periodic discharge system of the avian cecum may function nearly as uniformly as in the continuous turnover systems of the rumen

and some mammalian ceca.

The cecum varies in size and fill throughout the year in wild rock ptarmigan. In general the length, tissue weight and fill were greatest during winter while birds fed on the lowest quality foods and the cecum declined to its minimum annual size during summer when forage quality was highest. In spite of the changing volume of the cecum, the contribution of ME from cecal fermentation was similar during all seasons of the year. It was estimated that an average of 7% of the annual free living energy requirements of wild rock ptarmigan were available from VFA produced by microbial ferementation in the cecum, while only 4% of the free living requirements of willow ptarmigan were supplied during winter. Dry matter digestion in the cecum of captive rock ptarmigan accounted for approximately 2.5% of the total DM digested, thus energy available from cecal digestion provided approximately 2.5% of the caged, existence energy requirement. The large disparity in energy available from cecal functions in captive and wild rock ptarmigan can be partially accounted for by the significant reduction in cecum size that occurs in captive birds fed high quality diets. Maximum cecal fill in captive ptarmigan was less than half that observed in wild birds during winter. The cecum may have decreased to a size where increased cecal efficiency, as in wild birds during summer, can no longer yield the high rates of DM digestion and production of fermentation products. The decreased cecal fill and size observed during summer in wild ptarmigan and in captive ptarmigan, both feeding on high planes of nutrition, may be in response to improved digestibility and decreased

food consumption of these higher quality foods, which results in less DM passing from the small intestine into the hindgut and consequently reducing the flow of DM available for entry into the cecum.

The highly selective, sorting mechanism in the hindgut which allows the most digestible material to enter the avian cecum, results in a more efficient, lighter weight organ compared to ceca of mammalian herbivores in which all digesta fractions are diverted into the cecum. However, in spite of the efficient cecal filling mechanism of avian herbivores, the cecum for its relatively large size appears to provide only a small portion of the total energy required by the birds.