CELLULOSE DIGESTION AND METABOLISM BY CAPTIVE ROCK PTARMIGAN

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Abstract—1. Carbon-14 labeled cellulose was fed to rock ptarmigan to provide evidence of cellulose digestion and metabolism. Digestibility of cellulose and energy metabolized by ptarmigan fed a diet of 6 and 30% cellulose were determined by a feeding trial.

2. Recovery of 14CO₂ in expired gases from ptarmigan fed 14C labeled cellulose demonstrates the digestion and metabolism of cellulose by gut microbes and the ptarmigan.

3. Rapid recovery of 14CO₂ in expired gases suggested prececal digestion of cellulose.

4. Cellulose digestibility averaged 34%, and was not significantly different between groups of birds, however, total cellulose digestion was significantly different in birds fed 6 and 30% cellulose diets, 0.4 and 3.7 g/day, respectively.

5. Indirect evidence is presented which suggests cellulose digestion in the cecum is relatively complete.

6. Caged existence energy averaged 63 kcal/day and was not significantly different between birds fed low and high cellulose diets.

INTRODUCTION

Vertebrate animals are not capable of producing cellulases which are capable of hydrolyzing the 1-4 β linkage of cellulose and some other structural carbohydrates. Therefore, herbivorous birds rely on the symbiotic bacteria of the gut to digest cellulose and other complex carbohydrates (Halnan, 1949; Henning, 1929; Radeff, 1928; Ziswiler & Farner, 1972; Thornburn & Wilcox, 1965a,b). Evidence of microbial hydrolysis of cellulose was presented by Suomalainen & Arhimo (1945) who found cellulase activity in cultures from ceca of various tetraonids. The metabolism of carbohydrates by microbes of the gut is through fermentation yielding principally volatile fatty acids (VFA) and ethanol (Battie & Shrimpton, 1958; Shrimpton, 1963; Annison et al., 1968; McBee & West, 1969; Gasaway, 1975a,b). The contribution of VFA to free living energy requirements of willow and rock ptarmigan has been estimated at 4 and 7%, respectively (Gasaway, 1975a,b).

Estimates of cellulose and crude fiber digestibility vary widely with diets and avian species, ranging from 0 to 50% (Kaupp & Ivey, 1922; Radeff, 1928; Maas, 1934; Mangold, 1934; Dymsha et al., 1955; Halnan, 1949; Thornburn & Wilcox, 1965a). Most cellulose digestibility studies have been conducted using domestic species with relatively small ceca; some exceptions are studies of rock ptarmigan (Lagopus mutus) (Moss & Parkinson, 1975), red grouse (Lagopus lagopus scoticus) (Moss & Parkinson, 1972), ruffed grouse (Bonasa umbellus) and chukars (Alectoris graeca) (Inman, 1973).

Disappearance of cellulose from the digestive tract does not conclusively prove that the bird derived energy from the cellulose. Therefore, the present experiment was designed to determine if carbon-14 14C labeled cellulose was digested, metabolized and oxidized to CO₂ by rock ptarmigan. Since wild ptarmigan have adapted to a relatively high cellulose and fiber diet, compared to grain or fruit eating species, it is of interest to compare their ability to utilize cellulose as an energy source. In the present study digestibility trials were used to estimate total cellulose digestion or disappearance and energy metabolized by rock ptarmigan fed high and low cellulose diets.

MATERIALS AND METHODS

Birds

Five 2-year-old captive rock ptarmigan were used in cellulose digestion trials. Three of the above five birds were used in the cellulose metabolism trial. These birds were raised from chicks captured in the summer of 1970 at Eagle Summit, Alaska (65°30' N, 145°25' W). They were maintained indoors at 18°C on a daily photoperiod of 18 hr.

Cellulose metabolism trial

Each ptarmigan was orally dosed with 0.5 ml solution of 1% methylene cellulose suspending 7 μCi of ground, purified cellulose uniformly labeled with 14C (International Chemical and Nuclear Corp., Irvine, Calif.). All birds were fed ad lib. until the time the dose was administered. The suspension had been acidified with HCL to release the volatile CO₂ then neutralized with KOH. The dose was administered by syringe through a polyethylene tube extended into the esophagus. Immediately following dosing, the bird was placed in a 10 gal air tight, plexiglass chamber. Carbon dioxide free air was drawn through the chamber by a pump. Carbon dioxide produced by the ptarmigan was periodically collected as a Ba(CO₃)₂ precipitate by bubbling chamber air through a solution of 0.5 N NaOH and 9% BaCl₂. Samples were collected for approx 5 min in duration at 15-45 min intervals during the 10-11 hr period following administration of the labeled cellulose. Most frequent CO₂ sampling was carried out during the first 3 hr, the period of peak 14C recovery. The Ba(CO₃)₂ precipitate was filtered under suction, and rinsed with distilled water, ethanol and ether. A 35-50 mg sample of the dried Ba(CO₃)₂ was weighed and suspended in 5 ml scintillation cocktail (5 g PPO and 0.1 g POPOP/L toluene with 2%
Fig. 1. Specific activity of 14C in expired CO₂ from three rock ptarmigan fed uniformly labeled [14C]cellulose and maintained on Purina flight conditioner (60% cellulose). Cecal defecations occurred during the period indicated by C. Cab-O-Sil. Samples were radioassayed in a Nuclear Chicago, Mark I liquid scintillation system.

**Cellulose digestibility trial**

Apparent digestibility of food and cellulose was estimated in two ptarmigan fed Purina flight conditioner (60% cellulose) and three birds fed Purina flight conditioner supplemented with powdered cellulose (30%, cellulose). All birds had been previously maintained on Purina flight conditioner, however, 90 days prior to the digestion trial the three birds were changed to the 30% cellulose diet. Two weeks prior to the experiment all birds were placed in individual wire mesh cages.

Food intake and excreta output were measured during a 3-day period. Excreta was separated into droppings of intestinal and cecal origin, oven dried and weighed. Apparent digestibility of the diets was estimated by food intake minus excreta output divided by intake. Cellulose content of food, intestinal and cecal excreta was determined (Crampton & Maynard, 1938) and total cellulose digestion was estimated by the difference between cellulose intake and cellulose excretion. Metabolized energy was obtained by subtracting the caloric energy of excreta from that of food consumption.

**RESULTS**

Digestion and oxidation of the 14C labeled cellulose occurred within 15-25 min based on the recovery of 14C in the expired CO₂ (Fig. 1). Peak concentration of 14C in exhaled gases occurred 100-150 min after ingestion and were followed by a rapid decline in concentration, reaching low levels 10-11 hr after ingestion (Fig. 1).

Peak 14C specific activity varied considerably. Defecation of labeled cellulose from the cecum during a period when rapid digestion was occurring may have resulted in the variability of peak 14C specific activity (Fig. 1).

Apparent digestibility of the 60% cellulose diet (60%.) was significantly greater (P < 0.05) than the digestibility of the 30%, cellulose diet (50%,) (Table 1). This difference in apparent digestibility of food was due to the relatively low and similar cellulose digestibility (31 and 36%,) determined for each group of ptarmigan (Table 1). However, the total digestion of cellulose was significantly different for ptarmigan fed the 6 and 30%, cellulose diets. Birds fed the 30%, cellulose diet digested an average of 3.7 g cellulose/day or 9 times more cellulose than birds fed the 6%, diet (Table 1). The difference in total digestion of cellulose was clearly a result of cellulose intake being 8 times greater by birds fed the 30%, cellulose diet. Energy consumed and excreted was significantly greater (P < 0.05) for birds fed the 30%, cellulose diet, however, the energy metabolized was not significantly different (Table 2).

**DISCUSSION**

The recovery of 14C in expired gases implies that cellulose was digested and oxidized to CO₂. However, microbial fermentation processes convert hexose to VFA as the principal end products and yield as a by product CO₂ (Beattie & Shrimpton, 1958; Hungate, 1966; Annison et al., 1968) and likewise, CO₂ is produced from the oxidation of these VFA by the avian tissues (Annison et al., 1969). Therefore two sources of 14CO₂ exist, namely gut microbes and ptarmigan tissue, and these sources cannot be distinguished. Since bacteria are capable of metabolizing hexose (cellulose) to VFA and since VFA is oxidized

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<th>Table 1. Mean apparent digestibility of dry matter (DM) and cellulose by captive rock ptarmigan</th>
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<td>Cellulose content of diet (%)</td>
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*Mean (standard deviation). Values are significantly different (P<0.05) between groups of birds.
by avian species, it follows that birds derive energy from cellulose.

Recovery of \(^{14}\)CO\(_2\) in respiratory gases commences within 15–20 min of ingestion of labeled cellulose. The transit time for liquid and DM markers through the intestine of rock ptarmigan was 54 and 84 min, respectively (Gasaway et al., 1975). Hence \(^{14}\)C appears in the respiratory gases prior to the labeled cellulose reaching the cecum suggesting that partial degradation and metabolism of cellulose by microbes occurs anterior to the cecum. Evidence does exist for fermentation anterior to the cecum and the most likely sites would be the crop and ilium. Cecotomized fowl have been reported to digest cellulose at levels approaching that for normal fowl (Thornburn & Wilcox, 1965a). Annison et al. (1968) have reported VFA in the proventriculus, gizzard and small intestine of the fowl, however the concentration of VFA was 0.05–0.1 of that found in the cecum. Also Moss & Parkinson (1972) report that concentrations of VFA in the posterior small intestine of wild red grouse were equal to that found in the cecum. Although in one wild rock ptarmigan, VFA concentrations in the small and large intestine were approx 0.05 the concentration found in the cecal contents (Gasaway, unpubl. data). In the domestic fowl, microbes were numerous in the crop, declined in numbers in the gizzard and anterior small intestine and again increased in the posterior small intestine; however, these microbial concentrations were small compared to those found in the cecum (Jayne-Williams & Fuller, 1971). Lactobacilli predominate in the crop of domestic fowl and lactic acid concentration in crop contents is positively correlated with their numbers (Jayne-Williams & Fuller, 1971). Contrary to these reports, McBee & West (1969) found no evidence for significant bacterial action in any section of the digestive tract of willow ptarmigan except the cecum. In spite of evidence indicating microbial digestion of carbohydrates in the anterior gut, the cecum is considered the principal site of digestion and fermentation by microbes (Annison et al., 1968) and the major site for cellulose digestion in rock ptarmigan (Moss & Parkinson, 1975).

Significant proportions of dietary cellulose are digested in avian species with well developed ceca. Rock ptarmigan digested 31–36% of dietary cellulose in the present study and up to 41% in studies by Moss & Parkinson (1975) which was greater than that reported in red grouse (14%) (Moss & Parkinson, 1972), ruffeled grouse, chukar and bobwhite quail (Colinus virginianus) (10–22%) (Inman, 1973).

Digestion and catabolism of cellulose occurs rapidly following ingestion by ptarmigan rather than at a uniform rate over the duration that the labeled cellulose remained in the intestine and cecum (Fig. 1). Entry of labeled cellulose into the cecum begins about 45 min after ingestion and is nearly complete 130 min later (Gasaway et al., 1975). From the specific activity curves (Fig. 1), it is suggested that either most labeled cellulose entering the cecum was rapidly digested or that only a portion of the cellulose was rapidly catabolized with the undigested portion eventually excreted.

The concept that cellulose digestion is rapid and nearly complete in the ptarmigan cecum is substantiated by low concentrations of cellulose in cecal droppings, e.g. less than 2%, in captive red grouse (Moss & Parkinson, 1972), approx 6% in spruce grouse (Canahtis canadenis) (Pendergast & Boag, 1971), 11% in captive rock ptarmigan (Moss & Parkinson, 1975), 15% in wild rock ptarmigan (Gasaway, unpubl. data) and 4–5 and 12–4% in the present study. Low concentrations of cellulose in cecal droppings could imply that very little cellulose enters the cecum, however if only small quantities of cellulose entered the cecum then the cellulose digested by birds in the present study and in those by Moss & Parkinson (1972, 1975) and Inman (1973) would have had to occur in the crop or intestine. This seems unlikely considering the magnitude of the cellulose digested, the rapid flow through the intestine and the low number of microbes in the crop and intestines as compared to the cecum. In addition, Moss & Parkinson (1972, 1975) found significant amounts of lignin in cecal droppings of red grouse and rock ptarmigan. Since lignin and cellulose are bonded in cell walls of plants, significant amounts of cellulose likely entered the cecum with the lignin. Hence, a high digestibility of cellulose in the cecum is likely to be the reason for the observed low cellulose concentration and low cellulose to lignin ratios in cecal droppings (Moss & Parkinson, 1972, 1975).

ME intake by rock ptarmigan averaged 63 kcal/day which was lower than the 67 kcal/day (when corrected for weight loss) found by Moss & Parkinson (1975) and the 71 kcal/day for the resting metabolic rate reported by West (1972).

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REFERENCES


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