$^{51}CrCl_3$ MOBILITY AND CELLULOSE DIGESTION IN THREE GALLINACEOUS SPECIES

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ABSTRACT

$^{51}CrCl_3$ MOBILITY AND CELLULOSE DIGESTION IN THREE GALLINACEOUS SPECIES

By

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The capabilities of ruffed grouse (Bonasa umbellus), chukar partridge (Alectoris graeca), and bobwhite quail (Colinis virginianus) to digest cellulose were compared. The role of the ceca in cellulose digestion was discussed relative to their morphological development and to the natural diets of the three species. The value of $^{51}CrCl_3$ as a marker for determining differential digestion in cecal and non-cecal gut portions was appraised.

No significant differences in percent cellulose digested were found among the three tested species when fed two diets, one containing 9.6 and another with 15.4 percent cellulose. Mean cellulose digestion ranged from 10.3 percent for chukars on the lower cellulose diet to 22.2 percent for bobwhites on the 15.4 percent cellulose diet.

In both chukars and grouse, approximately 90 percent of the cellulose entering the ceca for both diets was digested. The ceca of bobwhites, however, absorbed a lower percentage of cellulose than did the ceca of grouse and chukars. Cecal development is less pronounced in bobwhites and it was expected that they would digest less cellulose than grouse or chukars. Bobwhites digested only 60 percent or less of

the cellulose entering the ceca and some of this cellulose digestion may have occurred in the non-cecal gut.

For all species except bobwhites on the higher cellulose diet, dry matter metabolizability coefficients as calculated by the ratio of $^{51}CrCl_3$ in foods and non-cecal excreta were much lower than those calculated by the cellulose-ratio technique. For the low cellulose diet with all species, the coefficients were near 40 percent using the $^{51}CrCl_3$ method and near 50 percent using the cellulose technique. For the diet containing 15.4 percent cellulose, the mean dry matter metabolizability coefficients for non-cecal excreta using the $^{51}CrCl_3$ technique ranged from 11.0 percent for chukars to 43.6 percent for bobwhites. On the same diet, the cellulose technique resulted in dry matter metabolizabilities near 40 percent for all species. Cellulose seemed to have moved along with other food ingredients but $^{51}CrCl_3$ appeared differentially to leave the non-cecal gut portions and enter the ceca. Cellulose was considered to be a reliable digestive marker while $^{51}CrCl_3$ cannot be used for determining the relative distributions of digestion occurring in the cecal and non-cecal gut of birds.

Significantly lower total dry matter metabolizabilities were found for the higher cellulose diet than for the lower cellulose diet for grouse, 51.3 and 57.9 percent, respectively, and for chukars, 48.3 and 54.7 percent, respectively. No significant difference was found for bobwhites, however, between the total dry matter metabolizabilities of the two diets. The presence of cellulose in the diet seemed to inhibit the digestion of other food ingredients. For

bobwhites however this inhibition of digestion was masked by a significantly higher level of cellulose digestion on diet B than on diet A. The increased amount of cellulose in diet B did decrease total dry matter metabolizabilities of non-cellulose foods in the non-cecal gut for chukar partridge and bobwhites but not for grouse.

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INTRODUCTION

The capabilities of some herbivores to digest fibrous food materials may parallel food and habitat preferences. Ruminants are able to derive energy from cellulose which is less digestible or indigestible for other animals. Cellulose digestion has survival value since animals possessing that capability are utilizing vegetation not normally consumed by other animals, thus reducing competition for food.

Some gallinaceous birds eat vegetative parts that regularly include significant quantities of complex polysaccharides. Since many of these birds have well developed ceca (Leopold, 1953), it is frequently assumed that these structures were evolved to digest a high fiber diet. Bolton (1955) felt that fowl could digest only hemicellulose. Alpha-cellulose is a series of repeating cellobiose units (White et al., 1964) which would provide useful energy for birds if fermented by microorganisms inhabiting the gastrointestinal tract. Investigations of glucose metabolism in growing leghorn chicks indicated that no alpha-cellulose was digested (Anderson et al., 1958). Moss (1967) on the other hand determined that red grouse (Lagopus scoticus) digested as much as 40 percent of the alpha-cellulose in a natural diet containing 18 percent alpha-cellulose. Suomalainen and Arhimo (1945) found that cellulolysis (unspecified extent) occurred in the cecal digesta of four tetraonids. Thus, in at least some wild gallinaceous birds cellulose digestion apparently occurs. Similar data would be

helpful in appraising the nutritive potential of a variety of natural foods for other wild species.

The primary objective of the present study was to compare the relative abilities of three gallinaceous species to digest cellulose and to consider possible relationships of digestibility to cecal structure and to food selection. The ruffed grouse (Bonasa umbellus) was selected because it is a forest bird whose foods include aspen buds (Bump et al., 1947), which contain up to 28 percent crude fiber (Hill et al., 1968), and because grouse have exceptionally long ceca (Leopold, 1953; Semenov-Tian-Shanskii, 1960). The chukar partridge (Alectoris graeca), native to semi-arid regions in the Old World, was chosen because it is not a budding species but rather feeds upon seeds of a variety of domestic grains (Galbreath and Moreland, 1953; Harper et al., 1958) and yet its ceca are nearly as large as those of the grouse. The bobwhite quail (Colinis virginianus), in contrast is a farmland species that also eats grains and yet its cecal development is much less pronounced than in the grouse or chukar.

The second objective involved the reappraisal of the $^{51}CrCl_3$-ratio technique for determining the metabolizability of foods ingested by birds. Since indigestible food markers facilitate the collection of subsamples of the total excreta their use saves time and labor. Unfortunately, previously used markers, for example Cr_2O_3, have been tedious to quantify in food and feces (Dansky and Hill, 1952). $^{51}CrCl_3$ is a gamma emitting isotope and hence readily quantified. The half-life (27.8 days) is conveniently long for digestive studies and short enough to be safe for the test animals and experimentor.

Comparisons between the digestibility coefficients calculated

by the $^{51}CrCl_3$-ratio and total collection techniques have substantiated the advantages of chromium-51 in digestive studies of mammals (Mautz, 1971; Petrides and Stewart, 1968). Incomplete recovery of the isotope when fed to birds, however, indicated that an error was involved in the use of this material in avian studies (Duke, 1967; Inman, 1968). Because cecal droppings can be distinguished from intestinal excreta in gallinaceous birds, it was thought that $^{51}CrCl_3$ could function as a quantitative indicator of relative differential digestion in the cecal and non-cecal gut portions. As the study progressed, it became evident that observations of the isotope did not yield fully understandable results and more reliance was placed on cellulose as a marker. These differences in results yielded perplexing data.

METHODS

All birds used in these experiments were adults. They were held in wire cages, 36 × 18 × 36 centimeters in size, in an environmental room with standard light of 14 hours per day and approximately 24 degrees Centigrade temperature. Birds were given a week to acclimatize to these conditions and to the test diets.

The chukars and bobwhites were pen-raised but the grouse were wild, having been live-trapped the previous summer with lead traps (Lacinsky and Bailey, 1955) and raised to full size in captivity.

Two test diets were prepared to enable the assessment of cellulose digestion. The feed mixture in parts per hundred was:

Corn starch and/or cellulose	20.0
Ground corn	36.0
Soy bean meal	16.3
Fish meal	2.5
Alfalfa meal	6.5
Corn gluten meal	6.0
Hydrolyzed vegetable oil	2.5
Ground limestone	7.5
Dicalcium phosphate	1.8
Sodium chloride, iodized	.25
Choline chloride	.05
Vitamin and mineral premix	.60
	100.00

Vitamin and Mineral Premix	Supplies/kg.
Vitamin A (325,000 I.U./gm)	2200 IU
Vitamin D_3 (200,000 I.U./gm)	1100 IU
Menadione $NaHSO_3$	2.2 mg.
Riboflavin	3.0 mg.
Biotin	25.0 mcg.

Nicotinic acid	4	mg.
Vitamin B_{12}	5	mcg.
Ethoxyquin	125	mg.
Mg ($SO_4 \cdot H_2O$)	25	mg.
Zn (O)	8	mg.
Ground corn meal	to 6	gms.

Calculated Analysis

Protein	17.5%
Calcium	3.7%
Phosphorus, available	.52%

Diet A contained 10 parts of starch and 10 parts Solka Floc (Brown, Co., Chicago, Ill.) per hundred. Diet B contained 20 parts of Solka Floc per hundred and no starch.

The Crampton and Maynard (1938) method of cellulose analysis was used for foods and feces. Analysis of diet A revealed a 9.6 percent cellulose content while diet B was found to contain 15.4 percent. Since a 10 and 20 percent level of Solka Floc had been added to diets A and B respectively, the analyzed percentage of cellulose appeared unreliably low.

Standard samples with known amounts of Solka Floc yielded cellulose recoveries of 77 and 86 percent. Non-mercerized cotton (nearly 100 percent alpha-cellulose) was analyzed to determine whether the loss of cellulose was due to analytical error. The mean percentage recovery of cotton was only 85 percent. Therefore, the incomplete recovery was assumed to be due to a loss of cellulose as food samples were transferred between receptacles or to the digestion of some cellulose by the acids used in the analysis.

Analysis of three half-gram subsamples of the diet resulted in very similar determinations of cellulose levels (9.83, 9.24, and 9.71

percent) indicating good analytical precision. Analysis of known amounts of Solka Floc added to both food and fecal materials, furthermore, indicated nearly identical losses of Solka Floc regardless of whether food or feces was involved. Since the degree of cellulose digestion occurring in the birds was found by the difference between the amount of cellulose eaten and that found excreted and the same methods were used for both, the errors did not significantly affect the conclusions.

Foods marked with $^{51}CrCl_3$ were sprayed with an atomizer to a concentration of approximately 100 counts per minute per gram (cpm/gm) of food. After thorough mixing of the isotope and food, six random samples of about two grams each were weighed and counted in a Nuclear Chicago well-scintillation counter to get the exact isotope concentration. The counter was standardized daily with a standard sample of cesium-137 and corrections were made for normal decay and for background radiation.

Diets and water were offered ad libitum for ten days, during the last three of which all cecal and intestinal excreta were separated and collected daily for cellulose analysis. Excreta were dried at 95-100 degrees C., weighed, and frozen for later analysis.

Food intake was measured daily. Foods were then marked with $^{51}CrCl_3$ and the birds were fed for three additional days. Cecal and intestinal feces were separated and placed in the test tubes to a weight of approximately two grams. Feces were then dried and counted for radioactivity. During the first day of feeding, marked food was not used in any calculations since it requires a day for the isotope to reach a constant level in cecal droppings (Inman, 1968). All data and

computations listed are on a dry matter basis.

The level of cellulose in cecal and non-cecal feces was determined from two dry half-gram subsamples of the total cecal or non-cecal output after grinding in a mortar and pestle. Samples of the diets were ground in a Wiley mill for cellulose analysis. The total cellulose digested was determined from the formula:

Cellulose digested = total dry matter eaten × % cellulose - [(total non-cecal excreta × % cellulose) + (total cecal excreta × % cellulose)].

Feces and foods marked with $^{51}CrCl_3$ were used in the ratio technique to determine dry matter metabolizability coefficients according to the formula:

$$\text{Metabolizability coefficient (\%)} = \left[1 - \frac{\text{cpm/gm food}}{\text{cpm/gm feces}}\right] \times 100.$$

DIFFERENTIAL PASSAGE OF CELLULOSE AND $^{51}CrCl_3$ IN THREE NON-DOMESTIC GALLINACEOUS SPECIES

Studies of the apparent digestibility of foodstuffs have aided in determining the nutritional value of these foods. The techniques available, however, all have some undesirable aspects. The total-collection technique requires that the animal ingest food at some constant rate. The investigator must also collect feces for a long enough period to minimize the error resulting from day to day variation in passage rate of ingesta. Total volumes of feces can also become cumbersome in studies of larger animals.

Indigestible food markers have been employed as an alternative to total collection where the ratio of the marker to nutrients in food and feces is used to estimate nutrient digestibility. However, two of the most widely used markers, lignin and chromic oxide, require that the marker be quantified by laborious chemical procedures (Elam et al., 1962; Schurch et al., 1950).

Radioactive markers are easily detected and thus are convenient and labor-saving, and collection of all feces is not necessary. Radioactive chromium-51 EDTA has been used as a marker in studies with ruminants (Downes and MacDonald, 1964). Petrides (1968) used chromium-51 chloride ($^{51}CrCl_3$) for digestive studies of many wild mammals. The usefulness of $^{51}CrCl_3$ has been substantiated for mammals by Mautz (1971) who compared the $^{51}CrCl_3$ ratio technique to the total

collection technique in white-tailed deer (Odocoileus virginianus). However, $^{51}CrCl_3$ used in digestive studies of gallinaceous birds resulted in only a 90 percent recovery of the isotope (Duke, 1968; Inman, 1968). Therefore, in birds the ratio technique dry matter metabolizability coefficients did not equal those coefficients calculated by the total collection technique.

The present study was conducted to determine the feasibility of using $^{51}CrCl_3$ as a marker, despite the above-mentioned limitations, to measure differential digestion in the cecal and non-cecal gut portions of birds. The $^{51}CrCl_3$ ratio technique was also compared to the ratio of the cellulose in the diets and feces to determine whether the isotope and the cellulose both moved together in the gastro-intestinal tracts of bobwhite quail (Colinis virginianus), chukar partridge (Alectoris graeca), and ruffed grouse (Bonasa umbellus).

Materials and Methods

The isotope, $^{51}CrCl_3$, was applied to the diets using a spray atomizer which resulted in approximately 100 counts (as measured by a Nuclear Chicago well-scintillation counter) per minute per gram of food.

The diets were patterned after a chicken laying ration used at Michigan State University containing 17.5 percent protein and 5.5 percent fat by calculation. Cellulose (Solka Floc, Brown Co., Chicago, Ill.) was added at levels of 10.0 and 20.0 percent to derive two diets, A and B respectively.

The Crampton and Maynard (1938) method of cellulose analysis was used in analyzing both food and feces. Analysis of diet A revealed

a 9.6 percent cellulose content while diet B was found to contain 15.4 percent cellulose.

Since a 10 percent level of Solka Floc had been added to diet A, the analyzed percentage of cellulose appeared unreliably low. Analysis of Solka Floc resulted in cellulose recoveries of only 77 to 86 percent. Non-mercerized cotton was then analyzed to determine whether the loss of cellulose was a consequence of analytical error. The mean percentage recovery of cellulose from cotton was only 85 percent. Therefore, the incomplete recovery was considered to be due to a loss of cellulose as samples were transferred to and from receptacles and/or to digestion of some cellulose by the acids used in analysis.

Analysis of three half-gram subsamples of the diet, however, resulted in nearly identical levels of cellulose (9.8, 9.2, and 9.7 percent) indicating good analytical precision.

Analysis of known amounts of Solka Floc added to food and fecal materials indicated nearly identical losses of Solka Floc regardless of whether the medium was food or feces. Since the degree of cellulose digestion occurring in birds was found by difference between the total cellulose eaten and excreted, the analytical errors had a minimal effect on the conclusions.

Food and water were offered ad libitum. All feces were collected every 24 hours and separated into cecal or intestinal droppings (Leopold, 1953), dried, weighed, and counted for radioactivity. Following one week of acclimation to the test diet and location, the trial period continued for six days, the first three of which total feces were collected for calculation of total dry matter

metabolizability and cellulose analysis (Crampton and Maynard, 1938). Cellulose digested was calculated from the total cellulose ingested minus the total cellulose recovered in excreta. The last three days of the trial the food was marked with $^{51}CrCl_3$ to permit estimation of metabolizability by the ratio technique. Corrections for decay rate (T 1/2 = 27.8 days) of the isotope and background error were made when food and feces were counted. All data reported were on a dry matter basis.

Results and Discussion

Analysis of foods and non-cecal excreta for cellulose and $^{51}CrCl_3$ resulted in concentrations that could be used to calculate dry matter ratio metabolizability coefficients for the non-cecal excreta (Table 1). For example, the mean percentage of cellulose in the non-cecal excreta of chukars was 19.5 when the diet contained 9.6 percent cellulose. The dry matter metabolizability coefficient for foods not entering the ceca would then be 50.8 percent:

$$\left(1 - \frac{9.6}{19.5} \right) \times 100 = 50.8 \text{ percent}$$

The data for individual birds were used in this same way to enable calculations of mean metabolizability coefficients for each species. In the same way, the count per minute per gram (cpm/gm) of $^{51}CrCl_3$ was used to calculate dry matter metabolizabilities for non-cecal excreta.

The ratio method using the concentrations of cellulose in non-cecal excreta and food showed mean dry matter metabolizability coefficients for the non-cecal gut portions of 50.3, 50.0, and 48.9

Table 1. Dry matter metabolizability coefficients (mean ± s.e.) for the non-cecal gut as calculated by the $^{51}CrCl_3$-ratio and cellulose-ratio techniques for three gallinaceous species fed two levels of cellulose.

	Diet A (9.6% Cellulose)		Diet B (15.4% Cellulose)	
Species and Number	$^{51}CrCl_3$-ratio	Cellulose-ratio	$^{51}CrCl_3$-ratio	Cellulose-ratio
Chukar Partridge (8)	31.1 ± 1.4	50.3 ± 1.9	11.0 ± 1.7	39.0 ± 1.7
Ruffed Grouse (6)	43.3 ± 1.2	50.0 ± 2.5	23.1 ± 2.2	46.2 ± 1.5
Bobwhite Quail (8)	37.2 ± 1.3	48.9 ± 1.2	43.6 ± 0.5	39.0 ± 1.2

percent for diet A and 39.0, 46.2 and 39.0 percent for diet B for chukars, grouse, and bobwhites, respectively (Table 1). The cpm of $^{51}CrCl_3$ per gram of food and non-cecal feces, also used in the ratio technique, resulted in lower dry matter metabolizability coefficients for the non-cecal excreta. Means of 31.1, 43.3 and 37.2 percent were determined with diet A and 11.0, 23.1, and 43.6 percent with diet B for chukars, grouse, and bobwhites, respectively (Table 1).

Assuming that cellulose and $^{51}CrCl_3$ are thoroughly mixed with foodstuffs and do not separate during passage, the observed coefficients calculated by the cellulose and $^{51}CrCl_3$ ratios should have been equal for either diet since they measured the same degree of digestion occurring throughout the gut (excluding the ceca). This reasoning assumes that no cellulose digestion occurred in the small intestine or before. Suomalainen and Arhimo (1945) found in vitro digestion of an unspecified amount of cellulose in the gizzard contents but the ceca were clearly more effective. Also, Radeff (1928) found digestibility coefficients of crude fiber before and after cecectomy to be 17.1 and 0.0 percent and Henning (1929) found it to be 19.7 and 0.0 percent, respectively. With all other assumptions equal, the possible digestion or disappearance of cellulose in or before the small intestine should have produced lower metabolizability coefficients by the cellulose ratio than those actually observed.

To ascertain the reasons for the differences between the dry matter metabolizability coefficients by the $^{51}CrCl_3$ ratio and cellulose ratio techniques, a comparison of the quantitative passage of cellulose and $^{51}CrCl_3$ into the ceca was made. If the isotope mixes thoroughly with all foods, the percentage of ingested $^{51}CrCl_3$ recovered in cecal

excreta should equal the percentage of all foodstuffs that entered the ceca from the small intestine after digestion. For all chukars on diet A, a mean of 33.3 percent of the isotope ingested was recovered in cecal droppings.

The quantity of food that could potentially enter the ceca would be that which was left after digestion by the non-cecal gut portions. Where nutrients absorbed equals 31.1% (Table 1) and the total food eaten was 35.9 grams, therefore 23.7 grams would be available at the entrances of the ceca. According to the recovery of the isotope in the ceca 33.3 percent or 7.9 grams supposedly gained entrance.

Non-cecal excreta for chukars on diet A was found by analysis to contain 19.5% cellulose. Assuming that the food which entered the ceca had this same cellulose content then, (0.195 × 7.9 grams =) 1.54 grams of cellulose theoretically entered the ceca (Table 2).

However, by analysis only 0.03 grams of cellulose were recovered from the cecal droppings of chukars on diet A and total cellulose digestion was 0.38 grams. Assuming that all cellulose digestion occurred in the ceca and adding this quantity to that recovered in cecal droppings indicated that 0.41 grams (Table 2) of cellulose actually entered the ceca compared to 1.54 grams which theoretically entered (Table 2). Using the same calculations for grouse and bobwhites on diet A, the observed means for cellulose recovered in cecal droppings plus cellulose digestion equaled 0.97 grams and 0.69 grams, respectively (Table 2), whereas the theoretical amounts of cellulose which entered the ceca calculated from $^{51}CrCl_3$ and cellulose data, were 1.14 grams and 1.01 grams respectively (Table 2).

Table 2. The quantity of cellulose calculated to enter the ceca using $^{51}CrCl_3$ and cellulose concentrations as compared with the analyzed quantity of cellulose in the ceca for three gallinaceous species fed two levels of cellulose.

Species and Trial Period (Days)	Number of Birds	Quantity (Grams/Bird) of Cellulose Entering the Ceca			
		Diet A (9.6% Cellulose)		Diet B (15.4% Cellulose)	
		Calculated	Analyzed	Calculated	Analyzed
Chukar Partridge (2)	8	1.54	0.41	3.57	1.16
Ruffed Grouse (2)	6	1.14	0.97	1.89	1.05
Bobwhite Quail (3)	8	1.01	0.69	1.26	1.85

Except for bobwhites on diet B the calculated quantity of cellulose in the ceca was again greater than the analyzed quantity of cellulose in the ceca. 3.57, 1.89, and 1.26 grams of cellulose, respectively were calculated in the ceca as compared to 1.16, 1.05, and 1.85 grams of analyzed cellulose in the ceca of chukars, grouse, and bobwhites, respectively (Table 2).

These differences would seem to mean either that $^{51}CrCl_3$ becomes differentially concentrated in the ceca or that cellulose is restricted from entry there.

Consideration of the implication that cellulose was not entering the ceca in the same concentration as was found in non-cecal excreta would seem to be contrary to one of the presumed functions of the ceca, that is, crude fiber digestion. In addition, a mechanism which excludes cellulose from the ceca is difficult to fit into the concept of cecal digestion of fibrous materials. In this regard, the cecal aperture certainly seems sufficiently large enough to allow Solka Floc particles to enter without difficulty.

An attempt was made to ascertain whether cellulose entered the ceca at the same concentration as it was present in non-cecal excreta. For chukars on diet A, the non-cecal excreta measured 15.56 grams and the total ingesta was 35.86 grams. Using the dry matter metabolizability as calculated by the cellulose-ratio for non-cecal excreta, (Table 1) 18.04 grams of food were absorbed in the non-cecal gut portion. A total of 2.26 grams of remaining food must have entered the ceca, that is:

$$35.86 - (18.04 + 15.56) = 2.26$$

The analyzed quantity of cellulose in the ceca, assuming that all cellulose digestion occurred in the ceca, was 0.41 grams (Table 2). Therefore, the 2.26 grams of food entering the ceca must have contained ($\frac{0.41}{2.26} \times 100 =$) 18.14% cellulose (Table 3). The analyzed concentration of cellulose in non-cecal excreta for chukars on diet A was a similar 19.50% (Table 3).

The same calculations as noted above for the remaining species on diet A and B showed almost equal concentrations of cellulose in non-cecal excreta and in the food entering the ceca. Non-cecal excreta for grouse and bobwhites on diet A contained 19.4 and 18.9 percent cellulose respectively whereas the food calculated to enter the ceca contained 18.2 and 18.9 percent cellulose (Table 3). For chukars, grouse and bobwhites on diet B the non-cecal excreta contained 25.5, 28.8, and 25.4 percent cellulose respectively (Table 3). The food entering the ceca contained 24.6, 28.1, and 25.2 percent cellulose respectively for chukars, grouse, and bobwhites (Table 3).

If cellulose had been preferentially kept out of the ceca, the non-cecal dry matter metabolizability coefficients as calculated by the cellulose ratio would have indicated an inflated volume of food absorbed. The volume of food calculated to enter the ceca therefore would have been low. The calculated concentration of cellulose in food entering the ceca would then have been greater than the analyzed concentration of cellulose in non-cecal excreta. However, these compared cellulose concentrations were nearly equal for all species on both diets. Therefore, cellulose did enter the ceca in the same concentration as was found in non-cecal excreta, and the dry matter metabolizability coefficients for non-cecal excreta as calculated by

Table 3. Concentrations of cellulose analyzed in non-cecal excreta as compared with calculated (using cellulose data) in food entering the ceca for three gallinaceous species fed two levels of cellulose.

Species and Number	Percentages of Cellulose in Digesta			
	Diet A (9.6% Cellulose)		Diet B (15.4% Cellulose)	
	Analyzed in Non-cecal Excreta	Calculated for Food Entering Ceca	Analyzed in Non-cecal Excreta	Calculated for Food Entering Ceca
Chukar Partridge (8)	19.5	18.1	25.5	24.6
Ruffed Grouse (6)	19.4	18.2	28.8	28.1
Bobwhite Quail (8)	18.9	18.9	25.4	25.2

the cellulose-ratio are indicative of the digestion that occurred in the non-cecal gut.

The difference between the computed and measured quantities of cellulose entering the ceca (Table 2) must have been due to an inflated percentage of ingested $^{51}CrCl_3$ entering the ceca. Since $^{51}CrCl_3$ was water soluble the possibility existed that it moved with water into the ceca where water resorption occurs. This $^{51}CrCl_3$ movement would have lowered the non-cecal dry matter metabolizability coefficients as calculated by the $^{51}CrCl_3$-ratio technique (Table 1). In support of this, the dry matter metabolizability in the non-cecal gut as based on published research with domestic gallinaceous birds was thought to be higher than that indicated by the $^{51}CrCl_3$-ratio technique.

Yet for bobwhites on diet B the dry matter metabolizability coefficient for non-cecal excreta as calculated by the $^{51}CrCl_3$-ratio technique was larger than that calculated by the cellulose-ratio method (Table 1). The mobility of $^{51}CrCl_3$ into the ceca probably occurred to a lesser extent for diet B than for diet A, as evidenced by only 19.4 percent of the isotope in cecal excreta for diet B compared to 29.1 percent for diet A. In addition the quantity of cellulose calculated to enter the ceca using the $^{51}CrCl_3$ found in cecal excreta for diet B for bobwhites was higher than the analyzed quantity of cellulose in the ceca (Table 2). If $^{51}CrCl_3$ had passed proportionately with the food the compared quantities of cellulose would have been equal. Therefore, some cellulose may have been digested in the non-cecal gut of bobwhites on diet B.

Despite the data for bobwhites with diet B, in general $^{51}CrCl_3$ evidently was not a reliable marker for determining differential

digestion in the cecal and non-cecal gut of birds.

Implications of $^{51}CrCl_3$ Mobility

The movement of $^{51}CrCl_3$ into the ceca without equal food movement would invalidate the reported (Inman, 1968) degree of dry matter digestion calculated to occur in the ceca of ruffed grouse using $^{51}CrCl_3$. Unless later information shows that the present results are not applicable to species other than those tested here, relative digestions in the cecal and non-cecal gut of pheasants (Phasianus colchicus) as reported by Duke (1967) also may be distorted.

What mechanism(s) might affect the extent of the mobility of $^{51}CrCl_3$ is not certain from the data reported here. Conceivably water intake could affect the quantities of $^{51}CrCl_3$ moving into the ceca, as also could environmental or behavioral stress parameters affecting gut motility.

Possibly $^{51}CrCl_3$ could be used as a measure of water movement in the gut or of water conservation by resorption from the ceca. Interestingly, the dry matter metabolizability of the non-cecal gut as calculated by the $^{51}CrCl_3$-ratio for chukars was lower than for the other species for both diets (Table 1). Perhaps chukars, having evolved in semi-arid regions, tend to conserve water. Further research on $^{51}CrCl_3$ mobility in birds may be desirable.

Conclusions

When chukar partridge, ruffed grouse, and bobwhite quail were fed diets containing 9.6 and 15.4 percent cellulose and dosed with $^{51}CrCl_3$, the metabolizability coefficients for dry matter digested in the non-cecal gut were lower as calculated by the $^{51}CrCl_3$-ratio than when calculated by the cellulose-ratio technique. A differential movement of fluids carrying $^{51}CrCl_3$ out of the non-cecal gut portions into the ceca in amounts greater than the remaining dry matter is hypothesized as the explanation. In consequence, it is believed that $^{51}CrCl_3$ should not be considered a good indicator of quantitative differences between digestion in cecal or non-cecal gut portions of birds.

CELLULOSE DIGESTION IN THREE WILD GALLINACEOUS BIRDS AND ITS ECOLOGICAL IMPLICATIONS

Total Metabolizability as Related to Percentage Cellulose Digestion

Mean total dry matter metabolizability coefficients as calculated by the total collection technique were 54.7, 57.9, and 56.1 percent for chukars, grouse, and bobwhites respectively for diet A (Table 4). The $^{51}CrCl_3$-ratio technique for diet A resulted in lower total dry matter metabolizability coefficients, 51.3, 52.2, and 48.4 percent for chukars, grouse, and bobwhites, respectively (Table 4). The results for diet B were similar, where the total collection technique yielded mean dry matter metabolizabilities of 48.3, 51.3, and 54.0 percent whereas the ratio technique produced coefficients of 41.4, 34.3, and 50.6 percent for chukars, grouse, and bobwhites respectively (Table 4).

As previously reported (Inman, 1968; Duke, 1968), the $^{51}CrCl_3$-ratio resulted in lower coefficients than did the total collection technique when applied to birds. It was thought that incomplete recovery of the isotope (Inman, 1968) might be responsible. To ascertain whether the isotope had been absorbed and retained in body tissue, two chickens were fed food items dosed with $^{51}CrCl_3$. After the feeding, all droppings were collected and counted over several days until no further radioactivity could be detected in the excreta. The birds were then killed and sent to Argonne National Laboratories, Chicago, Illinois, for analysis. No appreciable radioactivity ($< .005\%$) was detected in the specimens by "whole body" counting. While time was not available in this study for further attempts to determine why an incomplete recovery of the isotope occurred, total collection dry matter metabolizability coefficients were used in

Table 4. Dry matter metabolizability coefficients (mean ± s.e.) determined by the total-collection (T.C.) and $^{51}CrCl_3$-ratio (R.) techniques for three gallinaceous species fed two cellulose levels.

Percent Cellulose in Diet		Chukar Partridge (8)*	Ruffed Grouse (6)	Bobwhite Quail (8)
9.6	T.C.	54.7 ± 1.4	57.9 ± 1.6	56.1 ± 1.0
(Diet A)	R.	51.3 ± 1.0	52.2 ± 0.9	48.4 ± 0.9
15.4	T.C.	48.3 ± 1.8	51.3 ± 1.4	54.0 ± 0.9
(Diet B)	R.	41.4 ± 1.2	34.3 ± 2.1	50.6 ± 0.4

*Number of birds.

appraising differences in digestion between species and diets.

No significant ($\alpha = .05$) differences (Seigle, 1956) appeared between mean dry matter metabolizabilities for the three species fed diet A. Bobwhites showed a significantly ($\alpha = .05$) higher metabolizability of diet B, however, than did chukars. There were no significant ($\alpha = .05$) differences in metabolizability between chukars and grouse or between bobwhites and grouse on diet B.

Bobwhites apparently were able to digest more of some food fraction than were chukars on diet B. Cellulose was the only food ingredient analyzed for digestibility. Mean total cellulose digestions for chukars (16.2 percent) and bobwhites (22.2 percent) on diet B were not significantly different at $\alpha = .05$ but were different at $\alpha = .20$ (Table 5). Thus there was an indication that bobwhites did digest more cellulose than did chukars on diet B. In fact, bobwhites had a significantly ($\alpha = .05$) higher percentage of cellulose digestion on diet B (22.2 percent) than on diet A (13.3 percent) (Table 5).

Since the diets differed only in cellulose content and since bobwhites digested a higher percentage of cellulose on diet B than on diet A, it might be anticipated that their metabolizability of total dry matter for diet B would be significantly higher than for diet A. This was not the case, however, because the coefficients were 56.1 and 54.0 percent for diets A and B respectively (Table 4) and showed no significant difference ($\alpha = .05$).

There was likewise no indication for grouse or chukars that the intensity of cellulose digestion affected total dry matter metabolizability in either diet. Grouse digested 19.6 percent of the cellulose on diet A and 14.6 percent on diet B, with no significant ($\alpha = .05$)

Table 5. Percentages of cellulose digested (mean ± s.e.) for three gallinaceous species fed two levels of cellulose.

Percent Cellulose in Diet	Chukar Partridge (N = 8)	Ruffed Grouse (N = 6)	Bobwhite Quail (N = 8)
9.6 (Diet A)	10.3 ± 2.9	19.6 ± 3.8	13.3 ± 2.6
15.4 (Diet B)	16.2 ± 2.4	14.6 ± 3.2	22.2 ± 2.5

difference (Table 5). Grouse therefore digested a larger quantity of cellulose on diet B than on diet A because diet B contained more cellulose. Yet their total dry matter metabolizability for diet A, 57.9 percent, was significantly higher (α = .05) than for diet B, 51.3 percent (Table 4).

Similarly, chukars digested 10.3 percent of the cellulose in diet A and 16.2 percent in diet B (Table 5). These results, too, were not significantly different (α = .05). But like the grouse, the 54.7 percent total dry matter metabolizability for chukars on diet A was significantly higher (α = .05) than the 48.3 percent metabolizability for diet B (Table 4). The presence of increased cellulose evidently adversely affected the absorption of other food ingredients.

In further analysis of this phenomenon, cellulose served as a marker in comparing the absorption of non-cellulose foods in the non-cecal gut in all species on each diet (Table 6). In order to equalize sample sizes, data for two birds each from the chukar partridge and grouse groups were not used in the total computations. These birds were dropped on the basis of their variable data as compared to the other birds of the same group.

For the remaining birds, ingested food was measured for each individual. The total quantity absorbed in the non-cecal gut was determined by multiplying the amount of ingested food by the individual dry matter metabolizability calculated by the cellulose ratio (Table 1). The quantities of non-cellulose and cellulose food materials were determined by multiplying the percentage of cellulose as found by analysis times the total material weight (Table 6). Cecal weights will be shown later but in this way it could be calculated how much ingested

Table 6. Metabolizability data (mean ± s.e.) for the non-cecal gut for three gallinaceous species fed two levels of cellulose where all cellulose is assumed to be digested in the ceca.

Species and Number	Ingested Materials (Gms/Bird/Day)	Diet A (9.6% Cellulose)			Diet B (15.4% Cellulose)		
		Ingested	Absorbed	Defecated	Ingested	Absorbed	Defecated
Chukar Partridge (6)	Total	17.14±1.49	8.42±0.98	7.51±.57	20.28±2.31	7.75±.83	10.43±1.15
	Non-cellulose	15.50±1.35	8.42±0.98	6.14±.43	17.76±1.96	7.75±.83	7.81±0.91
	Cellulose	1.64±0.14	0.00	1.37±.15	3.12±0.36	0.00	2.62±0.26
Ruffed Grouse (6)	Total	23.64±2.18	11.92±1.48	9.15±.73	22.08±1.37	10.24±.87	10.01±0.63
	Non-cellulose	21.37±1.97	11.92±1.48	7.36±.56	18.86±1.16	10.24±.87	7.11±0.42
	Cellulose	2.27±0.21	0.00	1.79±.21	3.40±0.21	0.00	2.90±0.23
Bobwhite Quail (6)	Total	9.63±0.39	4.66±0.27	3.66±.14	14.07±0.35	5.71±.28	6.19±0.28
	Non-cellulose	8.71±0.35	4.66±0.27	2.98±.11	11.90±0.29	5.71±.28	4.61±0.18
	Cellulose	0.92±0.04	0.00	0.68±.04	2.17±0.05	0.00	1.57±0.10

material was absorbed, passed into the ceca, or defecated.

The ingested and absorbed quantities (Table 6) were then used to determine the percentage absorption in the non-cecal gut (Table 7a). A two level factorial analysis of variance with Duncan's Multiple Range test (Steel and Torrie, 1960) was performed on the percentage absorption for non-cellulose foods (Table 7b). Percentages of absorption of non-cellulose foods in the chukar partridge, 53.7 and 45.8%, and bobwhites, 53.4 and 47.9%, were significantly higher for diet A than for diet B (Table 7a). Grouse, however, showed no decrease in the percentage absorption of non-cellulose foods from diet A, 54.6%, to diet B, 55.4% (Table 7a).

For chukars and bobwhites, the increased level of cellulose in diet B did decrease the absorption of non-cellulose foods. There is no evident rationale for grouse not showing this same decrease.

Cellulose Digestion as Related to Cecal Morphology and Feeding Habits

Since the ceca are large in all tetraonids and since grouse are a species which consume tree buds in winter, it has been assumed that cecal development evolved in order to enhance the digestion of natural fibrous diets. Bobwhites, on the other hand, are seed-eaters and have smaller ceca relative to their body size than do grouse or chukars. Yet no significant differences ($\alpha = .05$) were found between the percentages of total cellulose digested for diets A and B by the several species (Table 5).

To more clearly discern possible differences between the percentages of absorption of cellulose in the three species,

Table 7a. Percentage absorption (mean ± s.e.) of foods in the non-cecal gut for three gallinaceous species fed two levels of cellulose where all cellulose is assumed to be digested in the ceca.

Species and Number	Ingested Materials	Diet A (9.6% Cellulose)	Diet B (15.4% Cellulose)
Chukar Partridge (6)	Total	50.3 ± 1.9	39.0 ± 1.7
	Non-cellulose	53.7 ± 2.2	45.8 ± 2.7
	Cellulose	0.00	0.0
Ruffed Grouse (6)	Total	50.0 ± 2.5	46.2 ± 1.5
	Non-cellulose	54.6 ± 1.7	55.4 ± 2.8
	Cellulose	0.00	0.00
Bobwhite Quail (6)	Total	48.9 ± 1.2	39.0 ± 1.2
	Non-cellulose	53.4 ± 1.5	47.9 ± 1.4
	Cellulose	0.00	0.00

Table 7b. Two level factorial analysis of variance with Duncan's Multiple Range test for mean separations. Means underscored by the same line are not significantly different at the .05 level.

Source of Variation	df	SS	MS	F	
Treatments	5	465.81	93.16	3.93	$.005 < pF^{5}_{30} < .01$
A	2	188.95	94.47	3.29	$.05 < F^{2}_{30} < .10$
B	1	197.40	197.40	6.88	$.01 < F^{1}_{30} < .025$
AB	2	79.46	39.73	1.38	$.25 < F^{2}_{30} < .50$
Error	30	859.80	28.66		
Total	35	1325.62			

C_B	B_B	B_A	G_A	C_A	G_B
45.8	47.9	53.4	53.4	53.7	54.6

digestibility data for the ceca were computed. The quantity of material entering the ceca was determined (Table 8) by subtracting the absorbed and defecated quantities from that ingested (Table 6). The cecal defecations were subtracted from the amount entering the ceca to obtain the quantities absorbed there (Table 8).

The percentage absorption for the ingested materials in the ceca were then calculated (Table 9a) and analyses of the percentages of absorption in the cecal gut (Table 9b) were made in the same manner as those performed for the non-cecal gut (Table 7b)

For both diets the percentages of cellulose retained in the ceca for chukars, 86.7 and 94.4%, and for grouse, 93.8 and 89.0%, were significantly higher than for bobwhites, 54.8 and 74.8%.

That digestion of cellulose was higher in the ceca of grouse and chukars than in bobwhites was expected. Since the total percentage of cellulose digested was statistically equal for all species on both diets (Table 5), however the lower digestion of cellulose in the ceca of bobwhites was puzzling.

In order for the total cellulose digestion to equal the total cellulose digestion occurring in grouse and chukars, more cellulose would have had to enter the ceca of bobwhites.

But since the ceca of bobwhites are proportionately smaller than those of grouse and chukars, it did not seem possible that the ceca of bobwhites could accept voluminous quantities of food. Perhaps the ceca of bobwhites could accept more foods, including cellulose if the passage rate of foods entering the ceca was faster than is true for grouse and chukars. No passage rate data were available, however, for analysis.

Table 8. Digestibility data (mean ± s.e.) for the cecal gut for three gallinaceous species fed two levels of cellulose where all cellulose is assumed to be digested in the ceca.

Species and Number	Ingested Materials (Gms/Bird/Day)	Diet A (9.6% Cellulose)			Diet B (15.4% Cellulose)		
		Entering	Absorbed	Defecated	Entering	Absorbed	Defecated
Chukar Partridge (6)	Total	1.22±.29	0.71±.33	.51±.08	2.11±.60	1.55±.57	.56±.03
	Non-cellulose	0.99±.24	0.50±.25	.49±.07	1.60±.46	1.02±.41	.49±.03
	Cellulose	0.23±.05	0.21±.05	.02±.01	0.51±.13	0.49±.13	.02±.004
Ruffed Grouse (6)	Total	2.57±.67	1.84±.72	.72±.16	1.83±.39	1.23±.39	.60±.04
	Non-cellulose	2.09±.58	1.47±.60	.68±.14	1.32±.29	0.76±.27	.57±.05
	Cellulose	0.48±.10	0.44±.10	.05±.02	0.52±.10	0.49±.10	.03±.004
Bobwhite Quail (6)	Total	1.31±.16	0.63±.15	.67±.03	2.17±.34	1.41±.35	.76±.11
	Non-cellulose	1.07±.13	0.50±.13	.57±.02	1.57±.28	0.96±.28	.61±.07
	Cellulose	0.24±.03	0.13±.02	.10±.006	0.60±.08	0.45±.06	.15±.03

Table 9a. Percentage absorption (mean ± s.e.) of foods entering the ceca for three gallinaceous species fed two levels of cellulose where all cellulose is assumed to be digested in the ceca.

Species and Number	Ingested Materials	Diet A (9.6% Cellulose)	Diet B (15.4% Cellulose)
Chukar Partridge (6)	Total	44.1 ± 15.6	56.9 ± 12.2
	Non-cellulose	42.5 ± 13.4	33.1 ± 11.4
	Cellulose	86.7 ± 5.4	94.4 ± 2.1
Ruffed Grouse (6)	Total	55.8 ± 12.3	63.7 ± 12.1
	Non-cellulose	44.3 ± 10.7	61.9 ± 9.9
	Cellulose	93.8 ± 1.5	89.0 ± 5.8
Bobwhite Quail (6)	Total	44.4 ± 7.5	60.4 ± 8.9
	Non-cellulose	42.1 ± 8.4	52.0 ± 9.7
	Cellulose	54.8 ± 4.1	74.8 ± 4.0

Table 9b. Two level factorial analysis of variance with Duncan's Multiple Range test for mean separations. Means underscored by the same line are not significantly different at the .05 level.

Source of Variation	df	SS	MS	F	
Treatments	5	7428.27	1485.65	14.68	$pF^{5}_{30} < .001$
A	2	6460.77	3230.38	31.93	$F^{2}_{30} < .001$
B	1	782.13	782.13	7.73	$.005 < F^{1}_{30} < .01$
AB	2	185.37	92.68	< 1	
Error	30	3124.52	101.15		
Total	35	10552.79			

B_A	B_B	C_A	G_A	G_B	C_B
54.8	70.3	86.7	89.0	93.8	94.4

Another possibility is that some cellulose digestion did occur in the non-cecal gut of bobwhites. As discussed for diet B (Table 1) using the cellulose-ratio method the dry matter metabolizability coefficients for the non-cecal gut indicated that cellulose digestion did occur there. If it were true that cellulose digestion occurred to some extent in the non-cecal gut for bobwhites on both diets, the percentage absorption of cellulose in the ceca of bobwhites would have been even lower than that calculated for grouse and chukars. The total percentage of cellulose digested thus could have been equal for all species on both diets. This could also explain the increased cellulose digestion in the ceca for diet B, 70.3, as compared to diet A, 54.8, for bobwhites. In addition for bobwhites, the dry matter metabolizabilities in the non-cecal gut as calculated by the cellulose ratio (Table 1) would be lower than the actual digestion occurring there. But the conclusions as drawn from those previous data and the conclusions concerning the percentage absorption of cellulose in the ceca would remain the same.

In conclusion, the ceca of chukars and grouse were more efficient in cellulose digestion than the ceca of bobwhites; yet bobwhites digested as much total cellulose as did either of those species. Because bobwhites may have digested some cellulose in the non-cecal gut, they possibly could obtain as much energy per gram of natural fibrous diet as grouse or chukars. It might seem, therefore, that the large ceca of grouse and chukars were not more beneficial for total cellulose digestion than the entire gut of bobwhites.

The survival value of large ceca, of course, may not be due only to crude fiber digestive efficiency. Large ceca may enhance total

crude fiber digestion by accepting voluminous quantities of food. Prey species, especially, must maximize their potential energy intake in short periods of time. Hence, the possession of large ceca would enable a higher percentage of fibrous food intake to enter the ceca. Grouse and chukars have larger ceca relative to their body size than do bobwhites, and hence larger portions of diet could enter the ceca.

The calculated quantities of food entering the ceca (Table 8) were not proof that more food could enter when the ceca are larger, because a number of variable parameters affect this. First, the birds were caged and not fed a natural diet, hence the ceca could have atrophied. Evidence of change in cecal length with diet change was suggested for wild ruffed grouse (Pendergast, 1968). The refined diets fed here as a mash may also have caused a decrease in cecal size possibly to a greater extent for grouse and chukars than for bobwhites. Hence the ingestion of a natural diet by the three species could have possibly increased cecal size for the grouse and chukars to a greater extent than for bobwhites. At least for grouse, their normal diet contains more crude fiber and the ceca may be more capable of accommodating these diets. Accordingly, the calculated quantities of food entering the ceca may not have been the maximum capable of entering. Whether the total amounts of cellulose digested are indicative of the potential cellulose digestion for wild birds feeding on natural fibrous diets was not certain.

SUMMARY

Grouse, chukar partridges, and bobwhites were fed two diets dosed with the radioactive isotope, $^{51}CrCl_3$, and differing only in cellulose content (9.6 and 15.4 percent in diets A and B, respectively). Low concentrations of the isotope in non-cecal excreta and comparisons of $^{51}CrCl_3$ and cellulose mobility indicated that the isotope moved out of the main gut into the ceca. $^{51}CrCl_3$ was shown to be an unreliable marker for determining differential digestion in cecal and non-cecal gut portions of birds.

For some reasons, $^{51}CrCl_3$ showed less mobility for bobwhites fed diet B than for diet A. The $^{51}CrCl_3$-ratio dry matter metabolizabilities for non-cecal excreta for diet A were nearer the accepted digestive capacity of birds than was true in other experiments. A much lower percentage of the $^{51}CrCl_3$ was recovered in cecal excreta of diet B than that of diet A.

No significant differences in the percentages of cellulose digested were found among the species on either diet A or diet B. The ceca of bobwhites, however, were clearly less efficient in cellulose digestion than were those of grouse and chukars.

Lower efficiency of cellulose digestion by the ceca of bobwhites was expected. But since the total cellulose digestion was statistically equal in all species, bobwhites evidently obtained as much energy per gram of cellulose as did the grouse and chukars. Some

cellulose digestion must have occurred, therefore, in the non-cecal gut of bobwhites.

The presence of cellulose seemed to inhibit the digestion of other food ingredients. For all species except bobwhites, total metabolizability coefficients for diet B were lower than for diet A. The percentage of cellulose digested remained constant for grouse and chukars on both diets while that of bobwhites increased for diet B. For bobwhites therefore the increased cellulose digestion for diet B masked the decreased digestion of other foods. This was substantiated by the fact that the digestion of non-cellulose foods in the non-cecal gut of bobwhites was lower for diet B than diet A. Chukars, too, showed a lower digestion of non-cellulose foods for diet B than for diet A. It could not be explained for grouse however why the digestion of non-cellulose foods did not decrease from diet A to diet B when it was shown that total metabolizability did decrease.

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