COPROPHAGY IN THE RABBIT

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ONE FIGURE

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Coprophagy is practiced, at least under some conditions, by most rodents; but in the rabbit fecal eating has been stated to be a physiological habit with pecularities that imply a definite relation to the physiology of the digestive system (Frank, Hadeler and Harder, '51). It has been reported that the rabbit excretes a hard and a soft feces with virtually complete consumption of the soft type (Morot, 1882; Madsen, '39; Eden, '40; Southern, '40; Harder, '49); that the soft feces have a higher concentration of the B complex vitamins than does the hard type (Scheunert and Zimmerman, '52; Kulwich, Struglia and Pearson, '53); and that the composition of the soft feces is comparable to that of the cecal contents in protein, crude fiber and other proximate nutrients (Eden, '40; Harder, '49; Frank et al., '51; Olsen and Madsen, '44). None of these reports, however, satisfactorily explains the physiology of coprophagy with respect to its magnitude (Eden, '41), the variability between individuals, the effect of diet, or the effect on digestibility.

In this report data are presented relative to the effect of coprophagy on digestibility and on nitrogen utilization of two diets varying in content of roughage material and chemical composition. The physiology of coprophagy and the compositional differences in hard and soft feces are discussed. A method for the determination of the rate of coprophagy and the effect of diet on this rate will be presented elsewhere.

EXPERIMENTAL

A group of 4 Dutch rabbits was divided into pairs, a male and female, with each of the pairs fed one of two diets. The rabbits were placed on their respective diets at 4 weeks of age; at 14 weeks of age they were transferred to metabolism cages and established on approximately a maintenance level of feed intake. The established daily feed allotment was fed in equal portions morning and afternoon. One animal from each dietary treatment was chosen at random and placed in a stanchion. After a preliminary period of 10 days on a constant feed intake and under conditions of confinement, radioactive Cr_2O_3 thoroughly mixed in one day's feed was fed. The fecal excretions were then collected for 10 days from the stanchioned rabbits and for 30 days from the normal animals. The urine and feces for the 4th through the 10th day were composited in all periods for the digestibility and nitrogen balance determinations. At the completion of these collection periods, the situation was reversed for each animal and the procedure repeated. In the course of two years, three groups of 4 rabbits each were studied. The groups were treated similarly except that fecal collections were made mornings and afternoons with group I, mornings with group II, and every two hours for the first 8 days and twice daily thereafter for group III.

The feces were dried for 24 hours at 70°C., air dried for 7 days, weighed, and prepared for radioactive counting by grinding in a Wiley mill to pass a 20 mesh screen.

The basic composition of the two diets was dehydrated grass (roughage diet) and purified components (purified diet). The composition and analyses of these diets are given in table 1.

TABLE 1

Composition of diets

	PURIFIED	ROUGHAGE
	gm per 100 gm	
Crude casein [1]	25.0	...
Dextrin [2]	46.8	...
Cerelose	...	19.0
Dehydrated grass [3]	...	75.0
Hydrogenated vegetable oil [4]	8.0	...
Corn oil [5]	2.0	5.0
Ruffex [6]	10.0	...
Minerals [7]	5.0	...
Trace minerals (Cu, Mn, Fe and I) [8]	0.1	...
Na Cl	...	1.0
Fat soluble vitamins [9]	0.1	...
Water soluble vitamins [10]	3.0	...
Protein [11]	22.4	17.5
Ether extract	10.7	9.1
Ash	4.1	9.9
Lignin	0.49	3.8
Cellulose	10.2	21.0
Other carbohydrates	52.1	38.7

[1] National Casein Sales Co., Chicago, Illinois.

[2] White Dextrin N. F. V., Merck and Co., Inc.

[3] Cerograss, Cerophyl Laboratories, Kansas City, Missouri.

[4] Primex, Proctor and Gamble, Cincinnati, Ohio.

[5] Mazola, Corn Products Refining Co., New York, New York.

[6] Fisher Scientific Co., Pittsburgh, Pennsylvania.

[7] Hawk-Oser salt mixture.

[8] Fe $C_6H_5O_4 \cdot 1\frac{1}{2}$ H_2O, 453.85; $CuSO_4 \cdot 5H_2O$, 28.15; $MnSO_4 \cdot H_2O$, 16.50; KI, 1.50 gm per kilogram.

[9] Vitamin A palmitate, 666 I.U.; calciferol, 0.02 mg; alpha-tocopherol, 7.5 mg; Menadione, 0.075 mg per 100 gm of diet.

[10] Thiamine, 0.7; riboflavin, 0.7; calcium pantothenate, 1.5; pyridoxine, 0.7; niacin, 20.0; choline, 100.0; betaine, 100.0; inositol, 10.0; p-amino-benzoic acid, 0.2; folic acid, 0.10; biotin, 0.05 mg and vitamin B_{12}, 5 μg per 100 gm of diet.

[11] Analytical data are expressed on a dry matter basis.

RESULTS

The rabbits submitted to the restraint of the stanchion with minimum opposition. Restraint did not influence food consumption of the animals fed the roughage diet, and was decreased in only one rabbit receiving the purified diet. The stanchions effectively prevented the rabbits from eating feces.

A typical pattern of fecal excretion by a rabbit fed the roughage diet is shown in figure 1. The excretion of hard and soft feces is a consistent daily phenomenon both as to time and quantity. Under the conditions of this study, soft feces were eliminated at night and the hard feces during the day.

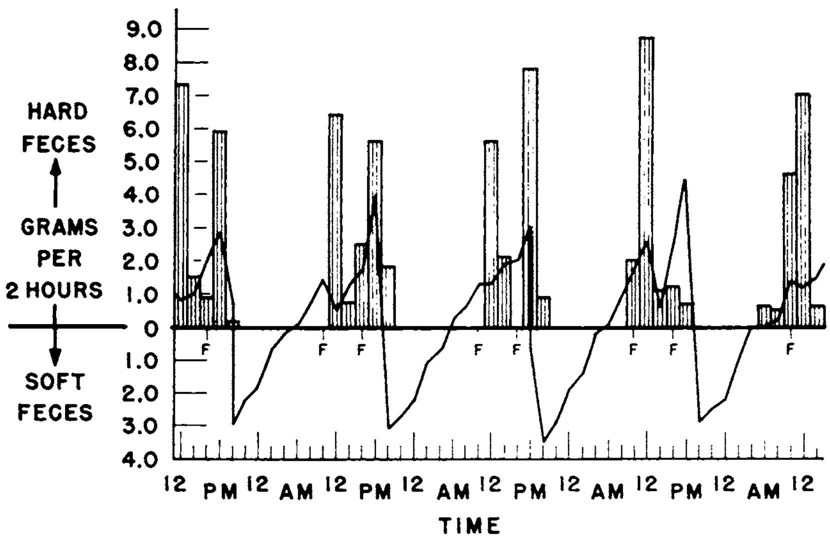

Fig. 1 Feces excreted in two-hour periods by a rabbit on the roughage diet. Bar diagram represents feces collected in free state. Line diagram represents feces collected in stanchioned state. Hard feces are plotted above the base line; soft feces below base line. F denotes time of feeding (10 A.M. and 4 P.M.).

The maximum excretion of soft feces occurred in the initial two hours then gradually decreased in quantity over an interval of 6 to 8 hours, and the elimination of hard feces gradually increased to a maximum. The feces collected in the normal period were entirely of the hard type. In this period the elimination of dry matter had two maxima; one possibly associated with the consumption of soft feces, and the other with feed intake.

The soft feces from the roughage diet were generally excreted as clusters of small, soft, moist, discrete pellets with a distinctive sheen. The hard feces of the same period were similar to the usually observed hard, round, dry pellets. The purified diet yielded feces that were difficult or impossible to differentiate into hard and soft fractions.

After the rabbits were removed from the stanchions, it was observed that the apparent quantity of fecal excretions had decreased. Quantitative collections indicated that after release from the stanchion the fecal excrement of the rabbits was less than 0.5 gm dry matter on the purified diet for

TABLE 2

Coefficients of apparent digestibility and retention of nitrogen by stanchioned and normal rabbits

	ROUGHAGE DIET			PURIFIED DIET		
	Stanch-ioned	Normal	Difference	Stanch-ioned	Normal	Difference
Dry matter	65.5	72.4	6.9 [1] ± 1.1 [2]	83.4	90.4	7.0 [1] ± 1.1 [2]
Protein	49.5	74.4	24.9 [1] ± 1.9	89.6	95.6	6.0 [1] ± 1.27
Ether extract	84.9	86.2	1.3 ± 0.61	97.7	99.1	1.4 [1] ± 0.23
Ash	54.2	61.8	7.4 [1] ± 1.2	51.3	76.0	24.7 [1] ± 4.9
Lignin	3.7	0.20	3.5 ± 5.8	...	...	... ...
Cellulose	36.4	33.6	2.8 ± 5.1	17.6	41.7	24.1 [1] ± 5.2
Other carbo-hydrates	93.1	94.2	1.1 ± 1.3	96.9	99.4	2.5 [3] ± 0.88
Nitrogen retained in body (mg day)	18.8	32.3	13.5 [1] ± 2.7	18.8	32.2	13.4 [1] ± 2.7

[1] Highly significant (P ± 0.01).
[2] Standard error of paired difference.
[3] Significant (P ± 0.05).

three to 6 days, and 2 to 6 gm for one to two days on the roughage diet. Whether this was actually a reduced excretion or an increased fecal consumption is not known.

The apparent digestibility of nutrients and retention of nitrogen in the stanchioned and normal periods for both diets is shown in table 2. The difference and the standard error of the difference between these paired variates (normal minus stanchioned) is indicated. The consumption of feces from the roughage diets improved the apparent digestibility of dry matter, protein, ash, and increased the retention of nitrogen (feed nitrogen minus that of the feces and urine). The digestibility of cellulose, ether extract and other carbohydrates was not influenced by ingestion of feces. On the purified diet coprophagy improved the digestibility of all nutrients studied and increased the retention of nitrogen.

The dry matter excreted on the roughage diet in the form of soft and hard feces in the stanchioned period and in the form of hard feces in the normal period is shown with its composition in table 3. Inspection of these data reveals that similarity of the composition of the hard feces derived from the roughage diet with and without coprophagy, and a considerable difference in the composition of the soft and hard feces from the stanchioned period in protein, lignin, cellulose and other carbohydrates. Similar data are presented for the purified diet except that the figures for the stanchioned period refer to the composition of the combined soft and hard feces. The dry matter eliminated in the stanchioned period contained more protein and other carbohydrates and less lignin and cellulose than did the dry matter excreted in the normal period.

Although the difference in the composition of the hard and soft feces has been observed by others, a reasonable explanation for this difference has not been advanced. Any postulation conceived must be physiologically tenable, and explain the cyclic excretion of hard and soft feces. It has been demonstrated (Eden, '40; Harder, '49; Frank et al., '51) that there is a marked similarity in the composition of the soft feces and the cecal contents. It is reasonable to presume, then, that soft feces originate from the cecum. Anatomically, however, all ingesta from the small intestine must enter the cecum through the ileo-cecal valve. If it is postulated that a segmented contraction of the spiral muscle of the cecum occurs associated with intestinal contents entering the cecum from the ileum, part of this material will be forced in the direction of the sacculated colon and part toward the blind end of the cecum. The ingesta forced into the colon by this

TABLE 3

Average daily composition of fecal dry matter

	ROUGHAGE DIET			PURIFIED DIET	
	Stanchioned				
	Soft feces	Hard feces	Normal	Stanchioned hard + soft	Normal
Dry matter, gm	6.89 ± 0.76[1]	9.824 ± 0.67[1]	13.67 ± 1.05[1]	4.55 ± 0.31[1]	2.91 ± 0.42[1]
Protein, %	37.41 ± 3.21	18.73 ± 1.71	16.6 ± 1.38	16.0 ± 0.35	10.3 ± 0.87
Ether extract, %	3.5 ± 0.12	4.3 ± 0.06	4.5 ± 0.16	1.5 ± 0.17	1.0 ± 0.30
Ash, %	13.1 ± 0.34	13.2 ± 0.81	13.9 ± 0.77	10.2 ± 0.63	9.7 ± 1.5
Lignin, %	7.5 ± 0.51	12.3 ± 0.40	12.7 ± 0.76	4.5 ± 0.25	8.7 ± 1.0
Cellulose, %	27.2 ± 7.60	46.6 ± 1.77	45.3 ± 1.70	58.2 ± 2.1	67.7 ± 0.89
Other carbohydrates, %	11.3 ± 1.57	4.9 ± 0.94	7.0 ± 2.16	9.7 ± 1.3	3.2 ± 1.1

Ratio soft : hard (stanchioned).
Lignin content = 0.61 ± 0.045.[1]
Specific activity = 0.51 ± 0.042.[1]

[1] Standard error.

action will form the principal substance of the hard feces with material that has in effect by-passed the cecum. The distribution of radioactivity in the gastrointestinal tract (table 4) supports such a movement of intestinal contents. The ingesta that remain in the cecum, then, form the soft feces when this organ, in a cyclic manner, undergoes a strong contraction of the spiral muscle. This action, perhaps associated with increased activity of the colon, carries the fecal material through the large intestine at a rate that results in the formation of small pellets with a high moisture content.

TABLE 4

Distribution of chromic oxide activity in the gastro-intestinal tract of the rabbit

Roughage diet, using data for stomach as a basis of reference	HOURS AFTER FEEDING		
	2	4	6
Stomach	1.0	1.0	1.0
Duodenum	..	0.4	..
Jejunum	0.3	0.6	0.3
Ileum	0.9	0.9	0.6
Lower cecum	0.7	0.6	0.6
Upper cecum	0.7	0.7	0.6
Appendix	0.1	0.0	0.5
Sacculated colon	0.6	0.8	0.6
Lower colon	0.1	0.8	1.2
Feces	0.0	0.0	0.2

Observation of intestinal activity in a laparotomy experiment indicated that this postulation of the physiology for the formation of hard and soft feces is essentially accurate.

In accordance with this postulation the differences in composition of the hard and soft feces must arise in the cecum. If it is assumed that a secretion is added to the cecal contents perhaps from the cecal wall, appendix, or both, a possible explanation is then available for the composition differences. If the secretion is largely mucoidal in nature, the protein composition of the soft feces would be increased and the lignin and radioactivity content decreased. The ratios of the lignin concentration in the soft and hard feces and of the specific activity (table 3) indicate a comparable reduction of these two fractions in the soft over that of the hard feces. Furthermore, since the reduction in ether extract and ash content of the soft feces is small, the postulated secretion must also contain lipid and mineral constituents. The increase in the other carbohydrate fraction of the soft feces over that present in the hard feces is further suggestive evidence for the mucoidal nature of the secretion.

In light of this postulation, the decrease in digestibility of protein and retention of nitrogen (table 2) associated with the prevention of coprophagy can be explained on the basis of a higher metabolic fecal nitrogen excretion. On the other hand, the coefficients obtained in the normal period suggest that this metabolic nitrogen is essentially completely digested when consumed.

The apparent digestibility of the cellulose of the roughage diet was not influenced by coprophagy, but the digestibility of the cellulose of the purified diet was approximately doubled by recirculation. The differences in the time the indigestible portion of the food remains in the body, and in fecal consumption rates may explain this apparent paradox. The cellulose of the purified diet was subject to a possible 9-fold increase in the length of time it was exposed to digestive processes in the normal period as compared to the cellulose of the roughage diet.[1]

The excretion of fecal dry matter and the relative dilution of lignin and increase in protein content of soft feces on the roughage and purified diets suggest that the mucoidal cecal secretion is lower on the purified diet than on the roughage diet. On the roughage diet, 6.9 gm of soft feces were eliminated daily with a dilution factor of approximately 0.5 or a presumed secretion in the cecum of 3.5 gm. On the purified diet, approximately 1.5 gm of soft feces were excreted with a dilution factor of 0.4 or a mucoidal secretion of 0.6 gm. This observation is in agreement with the known increase of metabolic fecal nitrogen with increasing fiber content of diets.

[1] Unpublished data.

DISCUSSION

These observations indicate that coprophagy has a profound effect on the utilization of nitrogen in the rabbit. Whether or not this effect can be directly related to the utilization of dietary nitrogen is a matter of conjecture at the present time. In order for the higher concentration of the nitrogen in the soft feces to be the result of the accumulation of feed residue nitrogen by bacterial action, a reduction in dry matter must be assumed. A reduction in dry matter would result in an increase in the lignin and radioactivity of the soft feces. Since the concentration of the lignin and the activity are reduced in the soft feces only two hypotheses are possible: the addition of nitrogen to the cecal contents or the greater removal of nitrogen in the colon from the hard feces than the soft feces.

While synthesis of bacterial protein occurs in the cecum, the nitrogen for this synthesis is contributed from both the feed residues and the postulated secreted protein. Studies relative to the synthesis of amino acids in the cecum are subject to misinterpretation until the question of the sources of nitrogen in the soft feces is resolved. Kulwich et al. ('54) recently reported that the soft feces of collared rabbits contained a greater proportion of a dose of S^{35} administered by stomach tube than did the hard feces. If it is assumed that the 12 μg dose of sulfate was essentially completely absorbed before reaching the cecum, the S^{35} in the soft feces would then have originated from the cecal secretions.

The possible nutritional benefits the rabbit derives from the apparent physiological habit of coprophagy do not necessarily reside only in the increased utilization of dietary nutrients. The studies of Scheunert and Zimmermann ('52), and Kulwich, Struglia and Pearson ('53), indicate that the vitamin nutrition of the rabbit is enhanced by this habit.

SUMMARY

The rates of coprophagy and the utilization of dietary nutrients were studied in the rabbit on two diets of different

compositions using radioactive Cr_2O_3 as an indicator. A possible physiological mechanism was postulated to explain the production of soft and hard feces, and a protein-containing cecal secretion was suggested to account for the compositional differences in the soft and hard feces.

The prevention of coprophagy resulted in an apparent decrease in protein digestibility and in nitrogen retention, and in the digestibility of dry matter on all diets studied. The effect of this habit on the utilization of other dietary nutrients depended on the diet studied. An increase in the digestibility of the cellulose of a purified type of diet was associated with the longer half-life of feed residues in the digestive tract of rabbits practicing coprophagy in comparison with those in which it was prevented.

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