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Jack A. Cranford

Virginia Polytechnic Institute and State University, jcranfor@vt.edu

E. O. Johnson

Virginia Polytechnic Institute and State University

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Effects of Coprophagy in Microtine Rodents

J. A. Cranford and E. O. Johnson

Department of Biology
Virginia Polytechnic Institute and State University
Blacksburg, Virginia 24061

Digestion and assimilation strategies of herbivorous mammals are diverse but fall into two major categories (Moir, 1968; Gartner and Pfaff, 1979; Hume and Warner, 1980). The most complex of which occurs in the lagomorphs and has been well studied. In contrast rodents exhibit great variability in diet and nutritional biology (Landry, 1970; Baker, 1971; Kenagy and Hoyt, 1980). Early reports of coprophagy by rodents were incidental or descriptive, and indicated it was infrequent (Howell and Gersh, 1935; Ingles, 1961; Wilkes, 1962; Hoover et al., 1969; Jarvis, 1981).

Rats mechanically prevented from reingesting feces showed reduced growth rates (Barnes et al., 1963). Presumably, some nutritive elements unavailable in the diet (such as B-complex vitamins and amino acids) are supplied through ingestion of products synthesized by endoflora harbored in the cecum of the lower digestive tract (Fridericia et al., 1927; Daft et al., 1963; Fitzgerald et al., 1964). Unfortunately, these micronutrients have not been determined with precision (Barnes, 1962; Barnes et al., 1963), but the nutritional benefits of coprophagy are probably quite similar for both rodents and lagomorphs (Kenagy and Hoyt, 1980).

Coprophagy in rodents is considered to be nutritionally beneficial, yet only a small amount of work has attempted to indicate the extent to which it occurs or the accompanying digestive mechanism in a rodent species (Kenagy and Hoyt, 1980). A recent investigation does indicate that reingestion behavior appears to be most frequent in herbivorous species, such as the microtines (Kenagy and Hoyt, 1980). Microtine rodents subsist primarily on forbs and grasses (Batzli and Cole, 1979) but do eat a wide variety of forage types (Zimmerman, 1965; Fleharty and Olson, 1969; Gill, 1977). Although few studies have closely examined the nutritional value of microtine forages, some dietary components appear to fluctuate with growing season (Cole and Batzli, 1979; Servello, 1981). Additionally, the nutritional quality of available forages may be affected by habitat manipulation (Cengel et al., 1978).

Few researchers have considered a relationship between changes in diet quality and the use of the cecum-coprophagy system found by rodents. Since free ranging animals may have a highly unpredictable diet which varies in quality over time, a mechanism compensating for dietary changes may involve coprophagy and postgastric fermentation processes. This study examined coprophagic behavior in response to diet quality for the meadow vole (Microtus pennsylvanicus) and the pine vole (Microtus pinetorum). The nutritional response of these animals to high and low quality diets was assessed after the

coprophagic component was eliminated from the digestive process. The nature of the nutritional response was determined by measuring food consumption, fecal production, diet digestibility, energy intake, and body weight dynamics.

MATERIALS AND METHODS

Experimental Animals: The microtines used in this study, meadow voles (Microtus pennsylvanicus) and pine voles (Microtus pinetorum), were obtained from outbred laboratory colonies at Virginia Polytechnic Institute and State University (Montgomery Co., VA). Experimental adult male meadow voles (weighing 40-60 g) and pine voles (weighing 20-30 g) were kept singly caged in Wahmann hanging cages (180x225x150 mm). When not in experimentally controlled diet studies, meadow voles were supplied with rabbit chow (Roanoke City Mills) and water *ad libitum*, while pine voles were supplied with rodent chow (Wayne Lab-Blox) and water *ad libitum*. Animal rooms were illuminated by fluorescent lights automatically controlled to provide a long photoperiod of 18L:6D and ambient air temperature was maintained at 20±1 C.

Two feeds were selected, one high quality (HQ) diet and one low quality (LQ) diet. The Wayne Lab-Blox rodent chow was used as the HQ diet; it contained a minimum of 24.0% crude protein, 4.0% crude fat, and a maximum of 4.5% crude fiber. Purina Horse Chow 100 was used as the LQ diet; it contained a minimum of 10.0% crude protein, 2.0% crude fat, and a maximum of 30.0% crude fiber. These chows were ground with a Wiley mill (1 mm screen) to eliminate differences in particle size between the two diets and to facilitate accurate weighing.

Coprophagy Prevention: Several approaches to the complete prevention of coprophagy in rats have been reported in the literature, often involving special cages or devices that were complicated and cumbersome (Hotzel and Barnes, 1966). A collar was devised to fit around the neck of a vole, preventing the animal from reaching the anus with its mouth or forefeet. Wire bottom cages permitted feces to fall through the floor upon elimination so that they were inaccessible to the animals. To control for possible physiological stress of wearing a collar, a control collar was designed to mimic the size and bulk of the coprophagy-prevention collars.

Coprophagy-prevention effects were examined for both species using a 2x2 factorial design with diet quality and coprophagic ability as factors. Data were analyzed by analysis of variance (ANOVA) procedures, and mean values were compared with Duncan's Multiple Range test, both applied using the SAS computer package (Helwig and Council, 1979). Eighteen animals randomly assigned to each diet class were divided into equal experimental and control groups. Experimental animals wore coprophagy prevention collars and control animals wore control collars, producing four treatment groups: noncoprophagous/HQ, noncoprophagous/LQ, coprophagous/HQ, and coprophagous/LQ.

Individual animals were weighed on day one of the pretrial period with an American Scientific Products model B1240-1 electronic balance (accurate to 0.1 g) and were provided with either the LQ or HQ diet ad libitum for the first five days. The digestion trial began on day six, when each animal was initially supplied with 35g of the LQ or HQ diet. Feed cups were replenished with premeasured 5g or 10g feed packets. The total amount given each day of the trial was recorded. This feeding procedure provided a constant supply of food in excess of daily needs even if large amounts were spilled or kicked from the feed cup. The true dry matter weight of each feed was determined after weighing replicate 10g samples which were oven dried at 60 C for 48 h. All packets to be used in one digestion trial were weighed at that same time as temporal changes in relative humidity would alter food packet weight. Following the digestion trial, all animals continued diet consumption ad libitum for six days and were weighed on the last day of the post-trial period.

Dropped feed and feces were collected daily during the digestion trial from trays beneath each cage. Feces and uneaten food were oven dried (60 C for 48 h), carefully sorted, and weighed on a Metler H31AR balance (accurate to 0.001g). Food consumption equaled the difference between dry weight of the total amount of food available and food remaining. Fecal production was determined on a dry weight basis. The apparent dry matter digestibility (ADMD) of each diet equaled 100 minus the percentage of consumed diet that was egested as feces. Individual body weight dynamics were determined for the entire experiment from initial and final body weights. An average body weight value was calculated for use in expressing food consumption and fecal production on a body weight basis. Finally, digestible energy (DE) was determined after samples of the food and feces were ground with a Wiley mill (Mesh size 40), pelleted, and combusted in a Parr adiabatic bomb calorimeter. Corrections were made for both fuse wire and nitric acid formation. DE intake (DEI) was calculated for each individual and expressed on a metabolic body weight basis (DEI/g^{0.75}).

RESULTS

Meadow voles: Of the four groups tested, coprophagous meadow voles maintained on the HQ diet had the greatest mean increase in body weight (4.21g) which was also the greatest mean percent weight gain (9.06%). Noncoprophagous voles on the LQ diet had the greatest mean decrease in body weight (-2.9g) which was also the greatest mean percent weight loss (-5.84%). The 2x2 ANOVA shows highly significant differences in body weight dynamics of voles maintained on different quality diets ($p < .001$). Coprophagous and noncoprophagous voles gained weight when on the HQ diet, but lost when on the LQ diet. Coprophagic ability also significantly influenced body weight dynamics (ANOVA, $p < .05$). On the HQ diet, coprophagous voles gained significantly more weight than did noncoprophagous voles (ANOVA, $p < .05$). On the LQ diet, noncoprophagous voles had a larger mean weight loss than did coprophagous voles, although these differences were not significant.

The ANOVA indicates that food consumption by meadow voles (g day^{-1} and $\text{g day}^{-1}\text{g}^{-1}$ vole) was significantly affected by diet quality ($p < .001$), and by coprophagic ability when consumption is expressed on a body weight basis ($\text{g day}^{-1}\text{g}^{-1}$, $p < .05$). The mean consumption of the HQ diet by coprophagous and noncoprophagous voles was 60% greater than LQ diet consumption. Within each diet class, mean consumption was slightly higher for noncoprophagous animals.

The ANOVA also shows that fecal production was similarly affected by the two factors. Diet quality was significant ($p < .001$) as mean fecal production on the LQ diet was over three times that of voles on the HQ diet. The ability to coprophage significantly affected fecal production (g day^{-1} , $p < .05$; $\text{g day}^{-1}\text{g}^{-1}$, $p < .05$), and noncoprophagous animals produced slightly greater amounts of feces than did coprophagous animals.

Diet quality and coprophagic ability also affected both indices of diet digestibility. Apparent dry matter digestibility (ADMD) was influenced by diet quality (ANOVA, $p < .001$) and coprophagic ability (ANOVA, $p < .05$). Within each coprophagic class, the mean ADMD values of the LQ diet were 40% lower than HQ diet values. Within each diet class, mean ADMD values of noncoprophagous voles were slightly lower than those of coprophagous voles. Digestible energy (DE) was also significantly affected by diet quality and coprophagic ability (ANOVA, $p < .001$). With respect to coprophagy, mean DE values on the LQ diet were 45% lower than those of voles on the HQ diet. Mean DE values within each diet class was slightly lower for noncoprophagous voles. DE intake was significantly affected only by diet quality (ANOVA, $p < .001$). Mean DE intake of the LQ diet was nearly 15% lower than that of the HQ diet, regardless of coprophagic ability.

Pine voles: Coprophagous pine voles maintained on the HQ diet had the greatest mean increase in body weight (1.41g) which was the greatest mean percent gain (5.55%). Noncoprophagous voles maintained on the LQ diet had the greatest mean decrease in body weight (-3.66g) which was the greatest mean percent loss (-11.88%). The ANOVA shows that body weight dynamics were significantly affected by diet quality (g , $p < .01$; $\%$, $p < .001$) and by coprophagic ability (g and $\%$, $p < .05$). Coprophagous and noncoprophagous animals displayed positive body weight dynamics on the HQ diet, and negative body weight changes on the LQ diet. However, noncoprophagous voles lost on the average significantly more weight when on the LQ diet than did coprophagous voles ($p < .05$).

The ANOVA indicates that the remaining parameters -- diet consumption, fecal production, ADMD, DE, and DE intake -- were significantly influenced only by diet quality. Regardless of coprophagic ability, pine voles on the LQ diet consumed on the average nearly 15% more food per day ($p < .05$) and 30% more per gram body weight per day ($p < .001$) than did voles on the HQ diet. Mean fecal production on the LQ diet was nearly three times that on the HQ diet ($p < .01$). Mean ADMA and DE values for the LQ diet were respectively 40% and 45% lower than HQ diet values. Mean DE intake of the LQ diet was more than 30% lower than that of the HQ diet.

DISCUSSION

Weight loss caused by the prevention of coprophagy was significant for both meadow and pine voles. The similar response in body weight dynamics due to coprophagy prevention demonstrates that the behavior is important in the maintenance of the nutritional status of these microtine rodents. Diet quality was also a conspicuous nutritional factor influencing weight changes. The four possible combinations of control and experimental treatments produced graded body weight changes, indicating that the individual factor effects were additive. Coprophagous animals on the HQ diet gained the most weight, and intermediate weight changes occurred in the remaining two combinations of coprophagic ability and diet quality. Although the effects of diet quality had higher levels of statistical significance than those for coprophagic ability, coprophagy prevention influenced body weight changes, irrespective of diet type.

The nutritional importance of coprophagy was readily demonstrated for both rodents; however, the nutritional response was not identical for the two species. The differences in food consumption, fecal production, and diet digestibility between coprophagous and noncoprophagous voles within each diet class were slight, but consistent. Noncoprophagous meadow voles had higher mean food consumption and fecal production values, and lower mean digestibility values than did coprophagous voles. In general, noncoprophagous meadow voles consumed more food and processed it less efficiently than did coprophagous voles. Similar effects attributable to coprophagy prevention were not observed in pine voles, for which food consumption and processing efficiency were affected only by diet quality.

The body weight changes observed in this study are consistent with previous reports of growth depression caused by coprophagy-prevention in rats (Barnes et al., 1963; Stillings and Hackler, 1966) and guinea pigs (Hintz, 1969). Barnes et al. (1963) found that growth depression was accompanied by lower food consumption; consequently, growth reduction was not attributed to lower food utilization efficiency, but to voluntary reduction in food consumption and to inaccessibility of growth stimulating factors present in the feces. However, Stillings and Hackler (1966) reported that noncoprophagous rats generally increased food consumption even though growth was depressed. In the present study, depression in food consumption by noncoprophagic pine voles was not observed, and noncoprophagic meadow voles actually consumed significantly greater amounts of food per gram body weight than did coprophagous voles. These results were important in establishing that food consumption by the voles was not physically restricted by the prevention collars. The prevention of coprophagy in meadow voles also led to lower diet digestibility.

Although coprophagy influenced diet digestibility in meadow voles, digestible energy intake per gram metabolic body weight (DE intake) by meadow and pine voles was not significantly affected by

coprophagy prevention. Increased food consumption by noncoprophagic meadow voles compensated for lower diet digestibility and maintained DE intake at levels similar to those of coprophagic voles within each diet class. Recycling feces would not be expected to automatically improve energy balance, since feces and food compete for intake, and feces contain less digestible energy than the original food source (Hornicke and Bjornhag, 1981). Reingestion could improve energy availability when the food supply is limited or of very low digestibility. Meadow voles in this study appeared to maintain energy intake at normal levels despite digestibility perturbations introduced by coprophagy prevention, and pine voles did not appear to experience appreciable energy loss from coprophagy prevention. Since these animals had an abundant food supply, coprophagy is probably most important for the acquisition of specific dietary nutrients, perhaps even at the expense of maximal energy intake. Therefore, body weight loss in meadow and pine voles resulting from coprophagy-prevention must be due to the loss of specific dietary factors provided through fecal reingestion.

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