INVESTIGATION OF SOME DIGESTIVE PARAMETERS OF THE WHITE-TAILED DEER USING THE RADIOISOTOPE ^{51}CHROMIUM

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ABSTRACT

INVESTIGATION OF SOME DIGESTIVE PARAMETERS OF THE WHITE-TAILED DEER USING THE RADIOISOTOPE ^{51}CHROMIUM

By

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Studies of the values of the radioisotope ^{51}Cr as a digestive marker in the white-tailed deer (Odocoileus virginianus) were made. The role of the rumen as a mixing organ, the relationships between food consumption and food passage rates, the effects of new surroundings, new foods, and starvation on digestive efficiency, and the relative energy values to the deer of three natural deer foods were appraised.

The major organ in which food mixing occurs is indeed the rumen. Using a rumen-fistulated deer ingesting a formulated standard diet, 5 to 30 minutes was required for a single dose of ^{51}Cr to become thoroughly mixed with food materials in the rumen. From studies of ^{51}Cr dilution, rumen dry matter content varied between 321 and 821 grams, with a mean of 547 grams.

Passage rates were studied mainly in animals fed ad libitum. In this work, a small known quantity of ^{51}Cr was

applied to 0.25 to 0.50 gram of food. Following ingestion of this item, fecal materials were collected and analyzed for ^{51}Cr content until the isotope had been 100 per cent excreted.

No significant correlation was observed between the rates of food consumption and food transit. Natural foods required somewhat longer to traverse the digestive tract than did the standard diet, but the difference also was not significant ($P > .10$).

As determined in an earlier study, spraying all foods ingested with ^{51}Cr allows calculation of digestibility coefficients by comparing the ^{51}Cr concentration in the food with that of fecal materials. In an effort to test a simpler method, a technique was tried in which only a limited number of 0.25 to 0.50 gram food items were dosed with radioactive materials. Unfortunately, this procedure resulted in highly variable fecal isotope excretion. It was concluded that a minimum of 2 radioactive particles would have to be ingested per hour in order to achieve success. This is impractical, hence all foods to be ingested should be sprayed evenly with the radioactive material.

Although a starvation diet of only 22.37 per cent of ad libitum ingestion caused a 17 per cent reduction in the body weight of the test deer, it had no significant effect on the digestibility of the standard diet.

Using ^{51}Cr, the time required before peak food utilization efficiency occurred was found to vary with different foods and previous feeding history. Nine to 12 days of confinement to the collection pen were required for animals to become adjusted digestively. Digestibility coefficients observed after this time were not significantly different from coefficients determined when these animals were in larger outdoor pens.

The 3 natural foods studied were aspen (Populus tremuloides) leaves, sumac (Rhus typhina) inflorescences, and bluegrass (Poa pratensis) clippings. They proved to be digested to nearly equal extents. The average dry matter digestibility coefficients for separate aspen, bluegrass, and sumac diets were 50.70, 49.42, and 54.17 per cent, respectively and well below the average digestibility coefficient of 65.68 per cent for the standard diet. Of the natural foods, sumac inflorescences were determined to provide the most energy. Animals consuming this food gained weight. Separate diets of aspen leaves and grass clippings yielded the deer near maintenance levels of energy. Combinations of these foods showed that interactions were present. Much more aspen-sumac mixture was consumed, for example, than would have been expected on the basis of values determined for the 2 species separately.

^{51}Cr was also found to yield pertinent data concerning the specific area of the gastrointestinal tract in which dry matter absorption occurs. By means of autopsies on 2 deer which had consumed a radioactive standard ration, it was determined that a surprisingly high proportion of materials leaving the small intestine enter the cecal pouch (> 70 per cent).

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INTRODUCTION

The rate and efficiency of energy transfer between producer and consumer organisms are important aspects in ecological studies of wild animals and in their adequate management. Animal nutritionists, too, have long been confronted with the need to measure the energy values of various rations.

Only a limited number of digestive studies have been carried out on wild species. Even though ungulates are one of the more important wild-herbivore groups, including the several deer species of economic significance, detailed information is lacking on energy conversion in these animals. The primary goal of this project was the further development (see Mautz, 1967) and evaluation of ^{51}chromium as a food label in digestion studies with the white-tailed deer (Odocoileus virginianus). In several of its phases, at least, this was a feasibility study to determine further suitable nutritional methodology. The nutritional data obtained are somewhat incidental to this exploration of procedures.

Digestion trials are primarily concerned with the extent to which a given diet is digested and absorbed and

with the length of time required for these to take place. The extent to which a food is absorbed by an animal is called the digestibility coefficient. This is normally determined by either the total collection or the ratio method. The total collection procedure involves determination of the dry weights of food eaten and of feces excreted from that food. With the ratio method, a constant level of an indigestible indicator is incorporated throughout the food eaten over a period of time, with the marker concentration in food and feces being compared. The gastrointestinal transit time is normally determined by marking a food sample with an indigestible substance and then measuring the time required for the marker to be defecated.

A number of different substances have been used in the past as food labels in ratio digestibility coefficient calculations and in passage rate analyses. Hoelzel (1930) made use of rubber particles, cotton thread, beads, seeds, and particles of aluminum, gold, silver, and steel in his study of passage rates in the rabbit, dog, cat, guinea pig, rat, mouse, hen, pigeon, monkey, and man. Other materials employed have included ferric oxide (Bergeim, 1966; Moore and Winter, 1934; and Tuckey et al., 1958), barium sulfate (Henry et al., 1933), celluloid particles (Mueller, 1956), and monastral blue (Lambourne, 1957). Several substances found naturally in plants have also been used as indices of passage rates and digestibility. These include oat hulls (Browne, 1922),

lignin (Forbes and Garrigus, 1948; Kane et al., 1952; Balch, 1957; and Gray et al., 1958), and chromogen (Reid, et al., 1952; and Kane et al., 1953).

In 1918, Edin suggested the use of chromic oxide (Cr_2O_3) as a food marker. Currently the most widely used food label, chromic oxide has been successfully used in nutritional studies of man (Krenla, 1947; and Irwin and Crampton, 1951), poultry (Olsson and Kihlen, 1948; Dansky and Hill, 1952; and Hill and Anderson, 1958), pigs (Schurch et al., 1952; and Moore, 1957) and sheep (Elam et al., 1962; and Johnson et al., 1964).

The use of a radioactive substance as a food marker has many advantages over stable indicators in nutritional studies. Even though radioisotopes can eliminate much of the time and labor involved in fecal analyses, until very recently they have been used only to a limited extent as food labels. Radioactive barium was used in digestive studies of the domestic fowl (Imabayshi et al., 1956), however, and Brandt and Thacker (1958) employed radioactive chromic oxide to study coprophagy in rabbits.

Recent work has determined the radioisotope ^{51}Cr to be a generally useful food label in nutritional studies of wild species. Using ^{51}Cr in 1964, Petrides (1968) studied passage rate and other digestive phenomena in the opossum (Didelphis virginiana), cotton rat (Sigmodon hispidus), bobcat (Lynx rufus), and other animals. Mautz (1967) and

Mautz and Petrides (1967) employed ^{51}Cr as a food label in nutritional studies of the white-tailed deer. Further work with the cotton rat (Petrides and Stewart, 1968) has confirmed that ^{51}Cr is a good food label for both passage rate and digestibility studies. Work with avian species (Duke, 1967 and Inman, 1969) has shown that ^{51}Cr is a valuable food label in passage rate studies but is not fully accurate in digestibility appraisals in birds.

There are several factors which make ^{51}Cr an ideal isotope for these types of digestive studies. Its half-life of 27.8 days is neither inconveniently short nor dangerously long. The physical, chemical, or spectrophotometric analyses required with stable compounds is eliminated since ^{51}Cr disintegrates with the emission of gamma rays allowing its ready detection and quantification. Foster (1963) describes ^{51}Cr as "one of the least hazardous radionuclides."

It is essential that labels used in digestibility and passage rate studies be substances which are not appreciably absorbed from the gastrointestinal tract. For $CrCl_3$ administered orally to white rats, Visek et al. (1953) reported that "less than 0.5 percent of the dose was absorbed from the gastrointestinal tract as indicated by tissue distribution studies." Roche et al. (1957) demonstrated that "practically negligible" amounts of ^{51}Cr introduced into the human gastrointestinal tract were absorbed. Mautz and Petrides (1967) found no detectable urine or tissue

radioactivity in white-tailed deer fed foods labeled with $^{51}CrCl_3$. Samples of tissues from experimental animals used in the current work, furthermore, were analyzed by Argonne National Laboratories and found to contain no ^{51}Cr at a level of 0.005 per cent.

The current study of the white-tailed deer was made in order to determine the usefulness of ^{51}Cr in ascertaining:

1. The particular role of the rumen in mixing, digesting, and passing food materials through the alimentary tract.

2. The relationship of the rate of food passage to food consumption, diet, and digestibility.

3. The lengths of time required for deer to attain a constant digestibility coefficient while changing from one diet to another and while adjusting to new surroundings.

4. The effect of a limited food intake on digestive efficiency.

5. The metabolizable energy of several deer browse species.

In addition, simplifications in technique were tested so as to learn how limited the number of radioactive food materials might be in order to yield the stable fecal isotope concentration necessary for digestibility coefficient measurements.

METHODS

Materials and Equipment

The compound $^{51}CrCl_3$ was the food marker used in this work. A Nuclear Chicago Well-Scintillation Detector System (DS-202V) with an 8725 Analyzer Scaler was employed to record the number of detectable disintegrations (counts) occurring in a preset period of time. All counts were corrected for decay and background radiation. Only those counts which were greater than twice the background count (normally 9-12 per minute) were used in computations.

Caloric values of all feeds and feces were determined with a Parr Oxygen Bomb Calorimeter. To obtain samples suitable for combustion, known volumes of urine were evaporated in petri dishes at 80-90^{o} C.

Deer used in this work were provided by the Michigan Department of Natural Resources. All were adult males and ranged from 80 to 200 pounds.

One exceptionally-tame deer was chosen for rumen fistulation studies of ^{51}Cr movements through the upper digestive tract. The fistula was inserted in a two-part surgical procedure by Dr. D. P. Purser of the Animal

Husbandry Department, Michigan State University. The preliminary phase was designated to cause adhesion of the rumen wall to the body wall. To do this, the abdominal wall was slit and both it and the adjacent rumen wall were first scraped to set up an inflamatory reaction and then sutured to each other. Care was taken at this stage not to puncture the rumen. Twenty days were allowed for the fusion to become complete. The second stage of the operation involved opening the rumen in the center of the fused area and inserting the cannula into the incision.

The cannula was of the sort commonly used in sheep and consisted of a short rubber tube with an internal flange. A rubber cork initially was used to plug the cannula. Eventually, however, a threaded, 3/4 inch diameter aluminum pipe with an easily-unscrewed plexiglass cap was fitted to the cannula opening. The rumen was opened by merely unscrewing the cap.

It is generally concluded that rumen fistulation has no abnormal effect on digestive mechanisms. When speaking of rumen fistulas in domestic animals, Hungate (1966; 176) stated that "the animals heal readily with little disturbance to their physiology." In deer, too, Hayes et al. (1964) reported that rumen fistulation does not significantly affect digestion coefficients.

Various investigators (Smith, 1950, 1952; Bissel et al., 1955; Deitz et al., 1962; and Cowan et al., 1969) have used

collection pens for nutritional studies of deer. For the present study, two collection pens were constructed similar to the one described by Mautz (1967). They were refined, however, with the addition of less-cumbersome collection devices. Each pen consisted of a 4 x 4 x 4 foot box mounted on stilts 4 feet tall (Figure 1). The walls of the pen were completely closed to avoid undue disturbance of the test animal by the attendant. A roof of boards placed approximately 1 to 2 inches apart admitted air and some light. The floor was formed by 3/4-inch flattened expanded-metal which allowed the ready passage of both feces and urine.

Beneath each pen, a large funnel of 1/4-inch hardware cloth deflected fecal materials into a small aluminum funnel located 30 inches beneath the pen floor and attached to the hardware cloth at only 2 points so as to swing freely. A sheet or polyethylene plastic film immediately beneath the hardware cloth deflected urine into eavestroughs which delivered it to a collecting receptacle for each pen.

To facilitate hourly separation of fecal materials for passage rate studies, a 3/4-inch plywood disc 4 feet in diameter was constructed for each pen. Each disc was bordered by 24 6-inch segments of 5-inch diameter stove pipe and was mounted so that while turning, its rim was directly beneath the aluminum feces-funnel (Figure 1). The aluminum funnel extended 1/2 to 1 inch into any given stove pipe. The tops of the stove pipes were notched on one side to allow easy

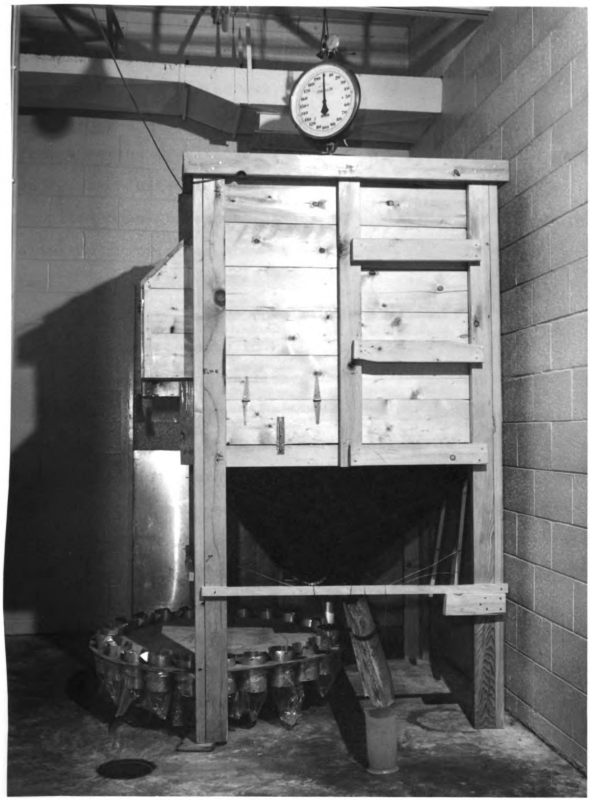
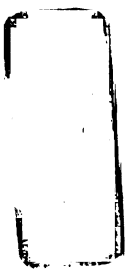


Figure 1. Collection pen used in digestive studies with white-tailed deer. Michigan State University, 1968.

entrance of the funnel. The fecal material dropped into plastic bags fastened by rubber bands to the bottom of each stove pipe. Each disc was rotated once per 24 hours, using a continuous-duty electric motor. Gear boxes constructed from a series of various sized lawn mower wheels and mounted on 1/2-inch axles (Figure 2) reduced the motor speed and supplied power leverage. As the discs moved, each hour the aluminum funnel came above a new stove pipe and collection bag.

In order to assure complete separation of urine from feces it was necessary to keep the hardwood cloth free of shed deer hair. To facilitate this, a 1-foot square opening was made in the floor of each pen. These openings were normally covered by slightly larger pieces of expanded metal. During cleaning operations a plywood sheet was lowered from the ceiling of the pen, partitioning the test animal from the area of the pen containing the opening. Through a small door in the wall of the pen the opening was exposed and the hardware cloth cleaned with a wire brush.

One of the pens contained a trap door on top which allowed a man to enter to collect rumen samples. With the other pen, it was possible to weigh the confined animal by an attached 600-pound spring scale. Block and tackle was arranged so that the pen could be hoisted off the ground, suspended from the scale. This could be accomplished easily by one person. By subtracting the weight of the empty pen,



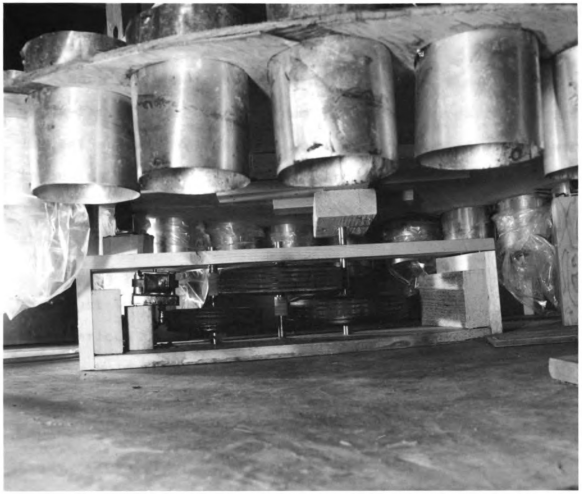


Figure 2. Collection apparatus used for separation of hourly defecations of white-tailed deer. Gear reduction unit shown. Michigan State University, 1968.

it was possible to keep weight records of the animal housed in this pen.

Each pen was found to be of sufficient size to hold a white-tailed deer ranging from 80 to 200 pounds. Even the largest animal had adequate room to turn around. All deer, including the 200 pound animal which was previously kept in a 40-acre enclosure, became surprisingly subdued during a short period of time in the collection pens.

The 2 pens were kept indoors in a 8.5 x 16 foot room. The light was controlled in this room to approximate outdoor photoperiods. Adjacent outdoor pens of the same size were used to hold additional animals.

A standard pelleted diet supplied by the Michigan Department of Natural Resources was used for much of this study. This diet, formulated by Dr. D. E. Ullrey, Animal Husbandry Department, Michigan State University, contained the following ingredients:

	Per cent	Pounds
Ground corn cobs	34.7	6,940
Ground shelled corn	29.5	5,900
Soybean meal 49	18.0	3,600
Linseed meal solution	10.0	2,000
Dehyd. alfalfa meal 17	3.0	600
Cane molasses	3.0	600
Corn oil	0.3	60
Regular Zn trace mineral salt	0.5	100
Ground limestone	0.5	100
Anhydrous sodium sulfate	0.25	50
Vitamin A, D and E premix*	0.25	50
	100.00	20,000

*Vitamin A, D and E premix

Pfizer 10P (10,000 IU vit. A/g)	6.62 lb.
Irradiated yeast 9F (9,000 IU vit. D/g)	0.5
Myvamix 125 (125,000 IU vit. E/lb)	3.2
Ground shelled corn	39.68
	50.00 lb.

Calculated analysis

Crude protein	16.6%
Calcium	0.38
Phosphorus	0.29
Sulfur	0.27

Natural foods used in this work were aspen (Populus tremuloides) leaves, sumac (Rhus typhina) influorescences and bluegrass (Poa pratensis) clippings. The aspen and sumac foods were collected over a 3-week period in July, 1968, at the Rose Lake Wildlife Research Station, 10 miles east of Lansing. Bluegrass clippings (Merion variety) were obtained July 15th to August 15th from a research plot maintained and mowed bi-weekly by the Michigan State University Turf Research Unit. These plant materials were stored frozen in polyethylene bags. To facilitate handling and mixing, the aspen and sumac were chopped by hammer mill to a size approximating that of the clipped grass.

Passage Rate Studies

Passage rates of each food were studied by feeding a single dose of ^{51}Cr applied directly to the surface of a 0.25 to 0.50 gram food item. ^{51}Cr levels of approximately 2 to 10 microcuries per trial were employed using pipettes

calibrated in lambdas (0.001 milliliter). Passage rate determinations in deer are independent of dose level in this range (Mautz, 1967). Nonlabeled food identical with the labeled item was fed ad libitum throughout the trial.

The fecal separation device was started at the time the isotope was fed. All droppings were collected until no further isotope was excreted. Two samples of 3 to 5 fecal pellets each were taken from each defecation and placed in tared test tubes. These samples were dried at 90-100° C to constant weight. This normally took a minimum of 24 hours. They were then weighed to the nearest thousandth gram and counted in the scintillation detector. The data for sample pellets were extrapolated to calculate the counts per minute per dry gram (c/m/g) and per total weight of each defecation.

In single-dose trials with the fistulated animal, the first rumen samples were taken immediately after ingestion of the labeled food. Several samples were taken during the first hour and hourly thereafter. On each occasion, the fistula cap was removed and a ½-inch diameter, 12-inch long copper tube fitted with a bulb type suction device was inserted. Samples of rumen contents were placed in test tubes. The animal readily submitted to collection procedures and became surprisingly unconcerned. Each rumen sampling took less than 5 minutes.

The average percentage reduction in ^{51}Cr concentration was determined for both rumen and fecal samples by least

squares regression analysis (Dixon and Massey, 1957:193). The time of 95 per cent fecal ^{51}Cr appearance was also recorded. This convention, which eliminates some of the problems and uncertainties of indicator detection at low levels, was first suggested by Castle (1956). This time was derived from percentage excretion curves constructed by plotting the accumulated percentage of indicator defecated against time. Mean retention times were also determined from these curves by summing the times of excretion of 10 per cent units of the marker, between 5 and 95 per cent, and dividing the total by 10 (Castle, 1956). Mean retention time is defined as the weighted average period that materials from a given meal take to traverse the tract. All materials present in the rumen at the time of isotope ingestion are considered to be the meal.

The relationship of rumen and fecal passage of ^{51}Cr was investigated for the standard diet. This diet was also used in the determination of effects of restricted food intake on passage rate. The passage rates of natural diets were investigated only at the ad libitum level of feeding.

Digestibility Studies

Determination of digestibility coefficients using the ratio technique required the feeding of a constant level of indicator for a period of several days until the fecal indicator concentration became stable. Then dry matter

digestibility coefficients were determined as:

$$\left(1 - \frac{\text{counts/minute/gram food}}{\text{counts/minute/gram feces}}\right) \times 100$$

Mautz (1967) successfully used the labeling technique of spraying deer foods with a uniform level of ^{51}Cr. Feeding food labeled in this manner yielded remarkably stable fecal isotope concentrations. Because of the amount of food involved with the present study, however, it was hoped that a more convenient labeling technique could be developed by feeding a limited number of individually-dosed food pellets. It was hoped that this would result in stable fecal isotope excretion and thus enable more ready calculation of digestibility coefficients.

To test this, the daily level of ^{51}Cr was distributed over various numbers of food pellets. Radioactive pellets were thoroughly mixed with nonlabeled portions of the daily ration prior to presentation to the animal. Each labeled pellet weighed approximately 0.25 to 0.50 gram. Normally 59 to 93 grams of feed were eaten by a deer per hour. Radioactive pellets were eaten at average rates of 3.8 to 41.5 per day.

All labeled pellets were counted to ascertain the amount of isotope being fed. The total dry weight of each daily ration also was recorded.

The fecal separation device was used for all continuous-dose trials and isotope concentration was measured in 2 samples from each defecation.

For comparative purposes, data for the calculation of digestibility via the total collection method were obtained simultaneously. This involved determining the dry weight of all feces excreted as well as of the food consumed over a period of 1 to several days. All feces excreted during these trials were weighed fresh and converted to dry weight by application of wet-dry correction factors. Total collection digestibility coefficients were calculated as:

$$\left(1 - \frac{\text{dry weight feces}}{\text{dry weight food}}\right) \times 100$$

Adjustment to Confined Conditions

The length of time required for an animal to become adjusted digestively to the collection pen was investigated for 2 animals on the standard diet. For these trials, a continuous level of isotope was fed for 21 days. While the animals were in collection pens, urine as well as fecal output was measured. By comparison of food and fecal concentrations of ^{51}Cr, it was possible to keep a record of digestibility coefficients throughout the trials.

Effects of Starvation

The effect of decreasing food levels on digestibility was carried out using the standard diet and a 200 pound animal. A continuous level of ^{51}Cr was fed for 28 days using 4 levels of food consumption: 80.8 grams/hour (ad libitum), 57.2 grams/hour, 38.2 grams/hour, and 19.1

grams/hour. Each level of feeding was maintained for approximately 1 week. By comparing food and fecal levels of isotope, any changes in digestibility coefficient between food consumption levels were detected. Periodic weighings of the test animal were carried out as described.

Natural Diets

Possible changes in digestibility caused by rapid introduction of a new food was investigated for each of the 3 natural foods used. This involved mixing a constant level of isotope throughout the food for several days beginning with the time of first food introduction. All defecations were collected and subjected to previously discussed procedures. Three deer were used in this phase, 1 being kept outdoors.

Digestibility coefficients were determined for each of the 3 natural foods and also for 3 mixed diets. The latter consisted of 1:1 wet-weight mixtures of sumac and grass, sumac and aspen, and grass and aspen.

Energy Values

In addition, gross energy digestibility values were calculated for each diet. Caloric values were obtained from bomb calorimetry of food and fecal samples and applied in the following formula:

Gross energy digestibility coefficient:

$$\left[1 - \left(\frac{\text{count/minute/gram food}}{\text{count/minute/gram feces}} \times \frac{\text{calories/gram feces}}{\text{calories/gram food}}\right)\right] \times 100$$

Metabolizable energy is defined as the amount of energy available to the animal after deduction of gross energy of the combined feces, urine, and combustible digestive gases. The measurement of methane and other gaseous digestive by-products was not possible in this study but the volume and caloric content of urine was determined for test animals held in the collection pens. With these data, the maximum gross energy metabolizability coefficient was estimated as:

$$\left[1 - \frac{(\text{feces defecated/hr.} \times \text{cal./g. feces} + \text{cal/hr. excreted as urine})}{\text{food consumed/hr.} \times \text{cal./g. food}}\right] \times 100$$

The energy lost in gases may deduct considerably, however, from this amount (Brody, 1945:82).

RESULTS AND DISCUSSION

Passage Rate Studies

Comparison of Rumen and Fecal ^{51}Cr Excretion

The constant mixing action of the rumen has been observed for many years in domestic ruminants. It is caused by contractions of the walls of the rumen and reticulum. Constant mixing serves to inoculate fresh ingesta with microorganisms present in the rumen, to aid comminution, to enhance nutrient absorption, and to assist passage of digesta to other areas of the digestive tract (Hungate, 1966:170).

The present studies confirmed that the rumen is the major site of digestive mixing in deer. Rumen samples, withdrawn periodically from the fistulated animal following ingestion of a single-dose of ^{51}Cr, disclosed a regular percentage decline in isotope concentration similar to that observed in subsequent fecal eliminations (Figure 3). There is no obvious explanation for this constant hourly decline except that as materials pass from the rumen, unlabeled foods are ingested which, upon mixing, cause a uniform dilution of the radioactive rumen contents. The rate of dilution shows some variation but nevertheless the

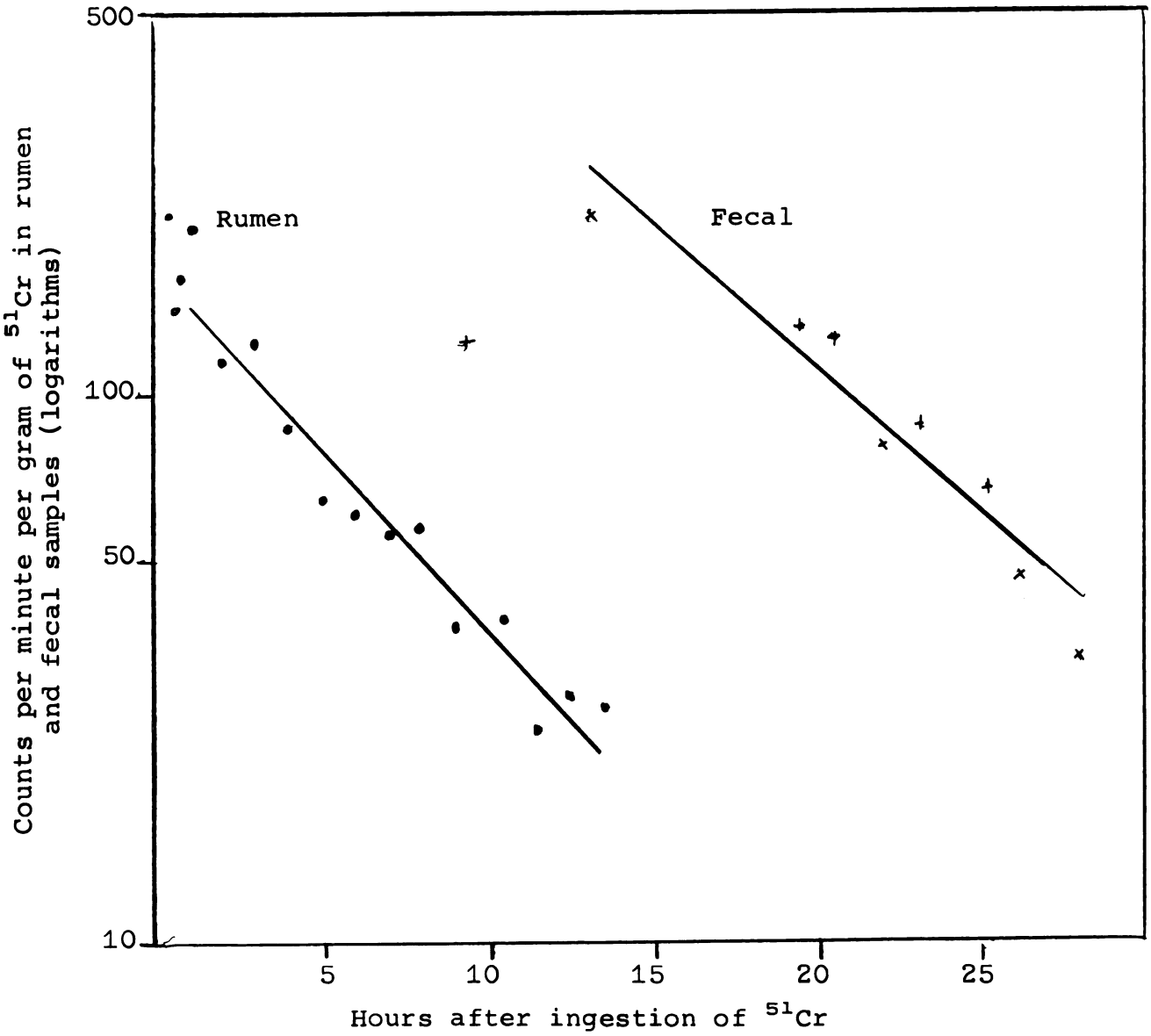


Figure 3. Rumen and fecal isotope elimination pattern in Deer II following ingestion of the standard diet with a 5 μc single dose of $^{51}CrCl_3$ (Trial 1, Table 1). Michigan State University, 1968.

removal slope is surprisingly constant during any one trial (Figure 3). This shows that in general, food is consumed on a regular and frequent basis, thorough mixing of digesta occurs in the rumen, and materials are passed from the rumen at a regular rate.

If no further dilution occurred beyond the rumen, the fecal decline in ^{51}Cr concentration should be at the same rate as that observed in the rumen. In nearly all tests with the fistulated specimen, however, the percentage hourly removal of ^{51}Cr from the rumen was higher than in the corresponding marked fecal eliminations (Table 1). A nonparametric paired t-test disclosed a significant difference at the 0.05 level between the means of the rumen and fecal passage rates. The lower fecal ^{51}Cr percentage excretion rate evidently was caused by a constant percentage dilution of rumen materials either with unmarked digesta or other materials in the remaining stomachs, intestines, and cecum.

For a deer on the standard diet, maximum isotope concentration in the rumen occurred 5 to 30 minutes after ingestion of the labeled food (Table 1). Evidently, the peak concentration of isotope occurs when it has become thoroughly mixed with digesta already present in the rumen. Early rumen samples showing lower than peak ^{51}Cr concentrations apparently were drawn prior to completion of the mixing process. True, there was a chance of withdrawing an early sample containing higher ^{51}Cr concentration than would occur after complete

Table 1. Percentage average hourly decline rates in ^{51}Cr concentrations of corresponding rumen and fecal samples. Based on data from a fistulated deer following ingestion of single doses of ^{51}Cr fed with a standard pelleted diet eaten ad libitum (Deer II). Michigan State University, 1968.

Trial	Rumen Digesta	Feces
1	13.69	12.14
2	16.06	10.66
3	30.23	24.45
4	23.65	*
5	13.12	8.54
6	11.92	5.29
7	25.78	5.03
8	6.01	6.89
9	*	7.46
Mean values	17.50	10.07

*Insufficient data.

mixing but this seems unlikely where the ingested radioactive materials represent 0.1 per cent or less of the total rumen contents.

According to Hungate (1966), the physical state of the digesta has much to do with the rapidity with which rumen contents are mixed. He states (1966:173) that "the speed of mixing decreases with increased particle size." As expected from this, the finely-ground pelleted ration did become mixed more rapidly than any of the natural foods used. Limited trials with aspen had a mean 'time of complete mixing' of 48 minutes while 1 trial with grass showed a mixing time of 35 minutes.

Rumen Dry Matter Content

By dividing the total count of the isotope ingested by the count per gram of isotope in the rumen after thorough mixing, the rumen dry matter content was calculated. Values of dry matter rumen content during 6 trials with the same fistulated animal on the standard diet varied from 321 to 821 grams, the mean being 547 grams (Table 2).

These data show considerable variation in the dry matter content of the rumen for a deer feeding ad libitum. In domestic ruminants, the minimal rumen content is reported (Balch and Line, 1957) to be rarely less than 50 per cent of maximum. The more variable results for deer could be due to the noncontinuous monitoring system used or to a real difference between deer and livestock.

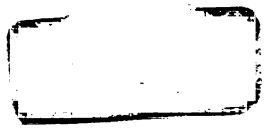


Table 2. Ingested ^{51}Cr levels, rumen isotope concentrations, and calculated rumen volumes for a rumen-fistulated white-tailed deer fed a standard pelleted diet (Deer II). Michigan State University, 1968.

Amount of ^{51}Cr ingested (count/minute) (=A)	Times and concentrations of early rumen samples		Calculated dry matter rumen content
	minutes after ingestion	c/m/g* (=B)	A/B (grams)
26,253	5	65	404
	15	65	
	30	59	
	60	47	
26,259	6	26	
	15	32	821
	30	22	
	60	27	
38,520	15	54	
	30	64	602
	45	54	
	60	44	
44,760	5	44	
	10	75	
	15	76	589
	30	68	
	60	60	
66,200	5	**	
	10	105	
	15	92	
	20	206	321
	25	64	
	30	142	
	45	165	
	60	200	

*c/m/g Count (detectable disintegrations) per minute per dry fram of digesta.

**Non-significant count.

Two trials with aspen and 1 with grass yielded calculated rumen dry matter contents of 522, 700, and 655 grams, respectively. The mean of these values (626 grams) is higher than the mean observed when the animal was feeding on the standard diet (547 grams). Since the standard diet used in the current study was more readily digested than any of the natural foods used (see beyond), this observation agrees with findings in domestic ruminants that rumen contents are reduced in easily digested rations (Yadawa et al., 1964).

Rumen Turnover Time

Hungate (1966:208) reported the turnover time of materials in the rumen to be equal to the period required for ingestion of an amount of dry matter equal to the dry matter in the rumen. This represents the average time that particles of digesta spend in the rumen. For the fistulated animal on the standard diet, the mean rate of food consumption was 64.6 grams per hour. Dividing the mean rumen volume of 547 grams (Table 2) by 64.6 yields an average time of 8.5 hours. So far as known, these data have not before been estimated for a wild ruminant. Castle (1956) working with the goat and using stained hay as a marker found the time of rumen turnover to be 19.4 hours.

Passage Time in the Alimentary Tract

Balch (1950) reported that the average time that particles of digesta spend in the rumen-reticulum is equal to the time

of 80 per cent fecal-indicator excretion minus the time of 5 per cent indicator excretion. Substituting 21.1 and 11.2 hours, respectively, it is estimated that 9.9 hours was required for the average food particle to pass through the rumen-reticulum of the fistulated deer on the standard diet. Balch also reported that the time of 5 per cent excretion was a good approximation of the time required for digesta to pass through the omasum, abomasum, and intestines. If this is true for deer, then 11.2 hours is required for this passage in the fistulated animal.

Natural foods, having a larger particle size and higher fiber content, would be expected to have slower rumen turnover times than the finely-ground standard diet (Hungate, 1966:220). The mean 5 and 80 per cent excretion times for the deer trials with natural foods were 12.5 and 26.6 hours respectively. Thus, according to Balchs' theory, the time of digesta passage through the rumen-reticulum and through the remaining portions of the alimentary tract were 14.4 and 12.5 hours respectively.

If Balchs' theory is valid for deer, natural diets required 4.2 hours longer to pass through the rumen-reticulum than did the standard diet. An additional 1.3 hours was needed for passage of natural foods through the remainder of the tract. The reason why natural foods have a greater increase in passage time through the rumen-reticulum than through the remainder of the alimentary tract doubtless

relates to the facts that in ruminants, the major digestion of dry matter occurs in the rumen and only food particles of small size pass into the omasum (Hungate, 1966:223).

Comparison of Passage Rate of Standard Diet and Natural Foods

Feeding a single dose of ^{51}Cr to animals consuming a natural food yielded a fecal excretion pattern similar in shape to that plotted for the standard pelleted diet (Figure 3) but showing the less-steep slopes indicative of less-rapid transit times (Table 3). The average of mean retention times for the natural diets eaten by Deer II was 21.4 hours compared to 17.1 hours for the standard diet (Table 3). Based on the nonparametric Mann Whitney U-test (Siegel, 1956: 119), however, this difference was significant only at $P < 0.172$. Similarly for Deer III, the average natural diet mean retention time of 22.4 hours was significantly greater than the 13.9 hours observed for the standard diet only at the 0.134 level.

While these levels of significance are low they do indicate that the natural diets, perhaps because of their more fibrous nature, tend to require a greater time of passage than does the more homogeneous standard mixture. Decreased passage rates may be due mainly to increased transit times through the rumen-reticulum as discussed. Two natural diet passage rate studies with the fistulated animal yielded rumen ^{51}Cr passage rates of 5.84 and 12.45 per cent per hour.

Table 3. Passage rate data of ^{51}Cr labeled meals for 2 deer fed the standard pelleted diet and several natural summer foods ad libitum. Michigan State University, 1968.

Deer	Diet	Percentage hourly ^{51}Cr defecation	First ^{51}Cr appearance in feces (hours)	95% passage time (hours)	Mean retention time (hours)
II	Standard*	10.14 (3.0)**	11.5 (1.2)	24.8	17.1 (1.7)
	Aspen	***	16.0	29.0	23.1
	Aspen	6.66	12.0	43.0	25.4
	Grass	8.09	15.0	24.0	18.0
	Grass	8.33	11.0	24.5	18.9
Average natural diets		7.69 (0.52)	13.5 (1.2 13.5 (1.2)	30.1(4.4)	21.4 (1.9)
III	Standard	14.90 (6.99)	11.0 (2.0)	19.5(2.0)	13.9 (2.0)
	Aspen	8.00	11.0	40.0	21.0
	Aspen	8.46	13.0	41.0	22.7
	Sumac	6.68	17.0	52.5	26.1
	Aspen & Sumac	9.16 (0.52)	10.0 (1.2)	28.8(4.8)	19.6 (1.4)
Average natural diets		8.08	12.8	40.6	22.4

*Average values for standard diet Table 4 .

**Standard error.

***Insufficient data.

These are significantly lower than those observed for the standard diet (Table 1) at $P < 0.178$.

Passage Rate Versus Food Consumption Level

The relationship between food consumption and passage rate was investigated for 3 deer on the standard diet. Parameters studied included the time of first and 95 per cent ^{51}Cr appearances, the percentage of isotope excreted per hour, and the mean retention time. The time at which 95 per cent isotope passage occurred and the mean retention time were calculated from percentage excretion curves (Figure 4). It is believed that the average time that food materials from a particular meal spend in the tract, the mean retention time, is the most important passage rate parameter.

For 1 of the animals used in these studies (Deer I) the food intake was progressively decreased in several stages, finally to a level 22.36 per cent of that normally consumed at ad libitum levels of feeding. Other deer were fed only ad libitum. No significant correlation ($P >> 0.10$) was found between the slope of isotope excretion or between the mean retention time and the amount of food consumed per hour (Table 4). ^{51}Cr analysis revealed that, at least in these studies, the rate of food passage was not affected significantly by the amounts of food eaten.

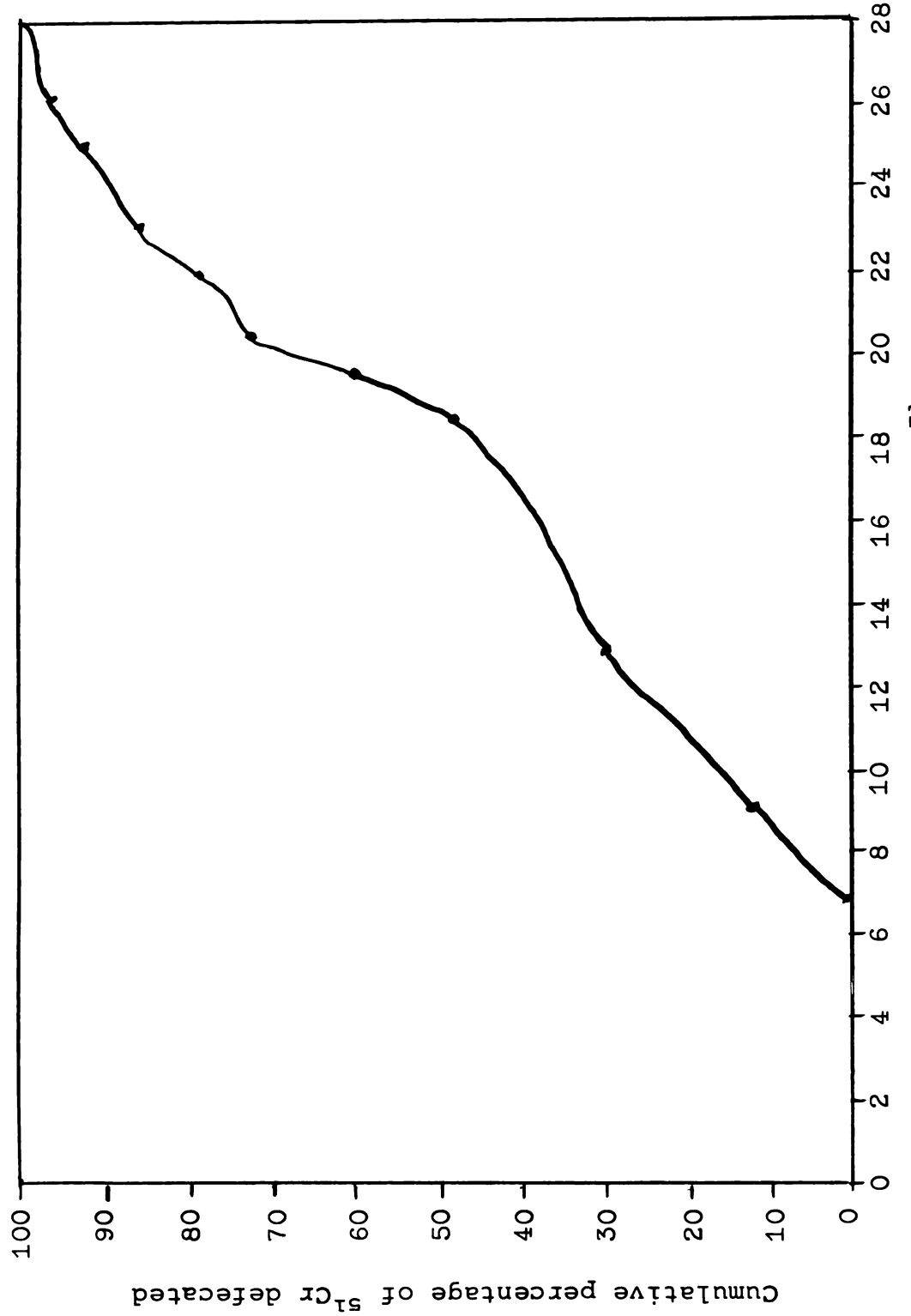


Figure 4. Percentage excretion curve of a single dose of ^{51}Cr for a deer ingesting the standard, pelleted diet (Deer II, single-dose trial 1, Table 1). Michigan State University, 1968.

Table 4. Level of food consumption as related to passage rate for 3 white-tailed deer on a standard pelleted diet. Michigan State University, 1968.

Deer	Grams/hour consumed	Per cent of isotope excreted in feces per hour	Time of first ^{51}Cr appearance in feces (hours)	95% excretion time (hours)	Mean retention time (hours)
I	93.1	7.63	23.5	44.9	30.8
	93.1	6.26	24.0	47.7	28.5
	66.5	4.90	24.0	47.5	29.0
	47.0	1.85	23.0	42.0	30.3
	20.8	2.23	23.0	58.9	32.3
	20.8	6.95	26.0	63.7	42.1
II	78.1	6.89	10.0	15.0	11.9
	69.3	5.03	12.0	23.0	15.8
	67.1	8.54	17.0	32.0	22.8
	65.1	5.29	9.0	20.5	13.6
	60.2	24.45	12.0	26.5	18.7
	47.6	10.66	9.0	32.0	19.5
III	69.4	21.84	13.0	17.5	14.1
	67.9	7.95	9.0	21.5	13.7

Digestibility Studies

Developmental Results

The feasibility of employing a simplified dosing technique in digestibility studies of deer was investigated by feeding 3 deer varying numbers of ^{51}Cr labeled 0.25 to 0.50 gram food particles per day. Since the food material tends to become thoroughly mixed, it was hoped that partial food labeling thus would yield stable fecal isotope concentrations similar to those observed when all ingested materials were labeled (Mautz, 1967).

For different trials on the standard diet, the number of radioactive items consumed per hour was varied between 0.16 and 1.72. Decreasing the number of radioactive items consumed per hour normally resulted in an increase in the variability of fecal isotope excretion (Table 5). This trend was by no means constant, however, and much unpredictable variability occurred within animals. When this experiment was performed, Deer I displayed a defecation pattern unlike that of the other animals used. While most animals showed no change in defecation rate between night and day, Deer I defecated only at night. This must have had an effect on fecal isotope variation because when this animal adopted a more typical defecation pattern the fecal isotope variability decreased.

Table 5. Variation in ^{51}Cr concentrations between different defecations from deer consuming various numbers of radioactive food particles mixed throughout the standard diet. Michigan State University, 1968.

Deer	Grams of nonradioactive food mixed with one radioactive food pellet (0.25-0.50 g)	Calculated radioactive food items ingested per hour	Variance between counts per minute of ^{51}Cr in different defecations	Standard errors for ^{51}Cr concentrations in different defecations
I	38.1	1.31	722.80	10.98
	97.6	0.51	1019.00	41.11
	155.4	0.32	1145.42	9.05
	310.8	0.16	1595.33	39.95
II	46.2	1.72	25.75	0.18
	62.2	1.28	63.29	2.21
	92.3	0.86	50.33	2.05
	138.5	0.57	60.16	1.26
III	46.2	1.28	126.32	1.27
	62.2	0.95	153.73	3.92
	92.3	0.64	217.75	4.66
	138.5	0.43	74.50	1.76
Average values when all food sprayed with uniform amount of ^{51}Cr (6 trials on 2 deer, Mautz, 1967)			21.62	0.16

In work carried out previously using the spray technique of applying ^{51}Cr to all food items ingested (Mautz, 1967), the variances of isotope concentration between different defecations ranged from 5.33 to 34.67, the mean being 21.62. The average standard error for these values was 0.16. These data represent 6 trials on 2 deer. With variation of this degree, it was found that accurate digestibility data could be based on only a few fecal samples.

In the current study, however, concentrating the total amount of isotope on a few food particles did not yield a stable level of fecal isotope. In none of these trials (Table 5) was variation between fecal isotope values observed which resulted in a standard error as small as that seen when all food materials were labeled. To be useful, this technique would require at least 2 radioactive food items to be consumed per hour.

The feasibility of applying the isotope in this manner rather than spraying all food items ingested would depend on the amount of food eaten by the test animal. Individually dosing 48 or more items per day would be less time consuming than the spraying method only perhaps, if an automatic pipetting mechanism were available and if the total amount of food ingested per day was great.

The variability of fecal isotope concentrations was also determined for an animal fed a decreasing amount of food per hour. Decreased levels of food consumption tended to

increase variability in fecal isotope concentration even though a stable number of radioactive items was consumed per hour (Table 6). The explanation for this is not known. Possibly there is less digesta mixing at the restricted consumption rates.

Thus, the level of food consumption as well as individual variability must be considered in determining the number of radioactive items per hour to feed. Reduced food consumption requires spreading the isotope over a greater number of individual items to yield a constant fecal isotope excretion.

Total Collection Method Versus Ratio Method

Because of increased variation in fecal isotope concentration induced by labeling small numbers of food items, it was not possible to obtain accurate digestibility coefficients from a limited number of defecations. Accurate digestibility coefficients were obtained, however, by lumping values from several defecations.

Good correlations between total collection and lumped-ratio values occurred only in trials on animals adjusted to both the diet and collection pen (Table 7). For trials in which test animals did not display constant levels of food intake, passage rate, or digestion, there were poor correlations between results of the 2 methods. This was due mainly to the changing levels of food consumption.

Table 6. Effect of restricted food consumption on fecal ^{51}Cr concentrations in an animal consuming a constant number of radioactive food pellets mixed throughout the standard diet. Michigan State University, 1968.

Deer	Grams of food consumed per hour	Radioactive food pellets consumed per hour	Variance between ^{51}Cr concentration in different defecations	Standard error of ^{51}Cr concentrations from different defecations
I	80.8*	0.44	133.25	2.11
	57.2	0.41	157.39	1.89
	38.2	0.41	335.59	2.62
	19.1	0.41	1617.29	7.22

*The ad libitum rate.

Table 7. Dry matter digestibility coefficients determined simultaneously by the ^{51}Cr ratio and total collection methods. Data for a deer consuming the standard diet (Deer I, trial 1:9). Michigan State University, 1968.

Period (days)	Ratio Method	Total Collection Method
2-4.4	69.09%	
0-4.6		71.93%
4.4-7.3	72.38	
4.6-7.4		68.50
7.3-8.3	69.78	
7.4-10.6		68.72
Means	71.92	70.06

The total collection method assumes a constant level of food ingestion and excretion. This was not the case in most trials carried out in this work, in which the animals were subjected to a new environment or to new diets. The ^{51}Cr ratio method does not require constant ingestion levels and, unless noted otherwise, digestibility coefficients presented beyond represent lumped ratio data.

Effects of Food Consumption Levels on Food Digestibility

An increase in digestibility with decreased food consumption levels was observed in cattle and sheep by Blaxter and Wainman (1961). The several levels of food intake in the preseny study, however, had no effect on gross energy digestibility or metabolizability coefficients for a deer on the standard pelleted diet (Table 8). Nearly identical digestibility coefficients were observed for the highest and lowest levels of food consumption. The slight drop in digestibility at the 2 intermediate levels of food intake were not significantly different from the extreme values.

The animal tested in this study was under extreme nutritional stress when its food was restricted. It lost weight at each successive level of restricted feeding and, by the end of the experiment, had lost 17 per cent of its initial weight.

Ullrey *et al*. (1969) found that feeding an amount of food 50 per cent of that consumed at ad libitum ingestion

Table 8. Gross energy digestibility and metabolizability coefficients for a deer at 4 levels of food consumption on the standard diet. Passage rate data are included. Michigan State University, 1968.

Dry grams of food ingested per hour	Number of days at given level of consumption	Weight in pounds of deer at end of given level of consumption	Gross energy digestibility coefficient	Gross energy met.* coef.	Percentage hourly fecal excretion of ^{51}Cr labeled meal**	Mean retention time**	95 per cent excretion time**
80.8	40.0	200	68.88	67.60	5.16 (1.24)	29.7 (1.1)	46.3 (1.4)
57.2	6.8	***	63.93	< 63.96			
38.2	7.8	182	66.02	60.76			
19.1	7.7	166	68.61	67.18	4.59 (7.36)	37.2 (4.9)	61.3 (7.4)

*Without correction for combustible gases.

**With standard error.

***Not measured.

levels caused no change in the dry matter digestibility coefficients of deer.

There are mixed reports in the literature on the effect of passage rate on digestibility. Blaxter et al. (1956) and Derrickson (1965) suggest that the digestibility of a food in ruminants can be predicted by its passage rate. Shellenberger and Kesler (1961), however, found that the digestibility of dry matter was not influenced by rate of passage. In the present studies, a somewhat decreased rate of passage resulted from low intake levels (Table 3) but this did not have marked effects on digestibility. The average mean retention times of the ^{51}Cr labeled meals for 80.8 and 19.1 grams per hour levels of food intake were 29.7 and 37.2 hours, respectively. These means are significantly different at a level of $P < 0.134$.

Effect of New Surroundings on Digestibility Coefficients

The length of time required for an animal's digestive mechanisms to adjust to collection pen conditions was determined during trials on 2 deer consuming the standard diet. For the first 4 days of the trial while the animals were outdoors, the weather was mild and the temperature was similar to that of the indoor collection pens. Deer II and Deer III then had dry matter digestibility coefficients of 67.38 per cent and 64.17 per cent, respectively.

When first transferred to the small pens, both animals showed marked decreases in digestibility coefficients of 23.68 and 7.81 per cent. Tending to rise gradually, by the 9 to 12 day of confinement both animals had digestibility coefficients approximating those observed at the outside locations (Table 9).

Texter et al. (1968:111,119) said that some emotions upset gastric secretions, gastric and intestinal motility, and hence digestive processes. It is not surprizing, therefore, that food digestibility decreased when the deer were first introduced to collection pens. They were visibly disturbed when first so confined.

No permanent change in the digestibility coefficients of a diet occurred between deer kept outdoors and those housed in the indoor collection pens, but 1 of the animals did show a permanent change in the level of food consumption. Deer III showed a transitory reduction in food consumption but regained outdoor levels of intake in 21 days (Table 9). Deer II had a significantly ($P < 0.064$) decreased level of consumption even 33 days after it was placed in the collection pen.

It may be that lack of exercise (Mayer et al., 1954, 1956) caused Deer II to undergo a more permanent reduction in level of food intake than Deer III. Both deer were quite active in the outdoor pens. Deer II became sedentary in the collection pen, however, while Deer III remained fairly active.

Table 9. Dry matter digestibility coefficients of 2 deer immediately preceding and after confinement to collection pens. Both animals ingested an ad libitum level of the standard, pelleted diet. Michigan State University, 1968.

Deer	Day of trial	Grams consumed per hour	Dry matter digestibility coefficient
II	1-4 (outdoors)	86.1	67.38
	5-8 (indoors on day 5)		43.70
	9-12		50.90
	13-16		66.00
	17-19	79.4	66.63
	20-25	63.2	
III	1-4 (outdoors)	67.0	64.17
	5-8 (indoors on day 5)		56.36
	9-12		59.80
	13-16		66.65
	17-19	59.0	64.73
	20-25	68.7	

Effect of Rapid Introduction of New Foods on Apparent Digestibility

Continuous digestion trials were run on 3 animals immediately preceding, during, and after rapid changes from 1 diet to another. No attempt was made to slowly introduce the animals to new foods. Each food when first introduced to the test animals had a markedly lower digestibility coefficient than was observed after the animal had been consuming the food for several days (Table 10). This confirmed that for deer, too, digestion trials must not be carried out before the animal involved has had time to adjust to the new diet. These delays probably ensue when a shift in diet by the host results in a subsequent change in the relative numbers of different species making up the symbiotic rumen community of bacteria and protozoa which digest the consumed plant materials. Like any other ecosystem, the trend in the rumen is toward stability, with those species most adapted to the prevailing environmental conditions becoming dominant over less well-suited species. To some degree the various enzyme systems important in digestive processes also become adjusted to a particular diet (Texter *et al.*, 1968: 183).

The deer used in this work and their symbionts, more readily adjusted the digestive mechanism to the grass and sumac diets than to the aspen diet (Table 10). The aspen diet, however, was the first natural food fed to Deer II.

Table 10. Dry matter and gross energy digestibility and metabolizability coefficients for a deer when first fed 3 natural foods. Michigan State University, 1968.

Diet	Deer	Number of days on diet	Dry grams per hour consumed	Dry matter digestibility coefficient	Gross Energy	
					Digestibility coefficients	Metabolizability coefficients
Aspen	II	2.5-3.5	36.2	17.30	16.24	9.91
		3.5-4.5	56.2	31.96	30.01	25.93
		7.4-9.5	65.7	51.54	48.50	45.82
Grass	II	2.0-3.0	36.8	19.07	22.09	16.15
		3.0-4.0	49.8	53.69	55.42	53.40
		7.7-12.2	50.3	50.63	52.47	50.60
		12.5-16.5	55.0	56.47	58.61	57.40
Grass	IV	1.0-2.0	12.2	22.45	20.67	---
		2.0-3.0	32.2	47.72	41.39	---
		7.0-8.0	36.7	47.37	41.04	---
Sumac	IV	2.8-3.8	44.42	45.68	41.32	---
		3.8-5.8	45.47	53.21	49.44	---

---Insufficient data.

Both with the grass diet and with sumac, these foods were preceded by another natural diet (of aspen or sumac). This may have been a significant factor in the shorter adjustment period observed for these new foods.

While food digestibility appeared to stabilize in most trials, the rate of food consumption continued to rise (Table 10). The stabilization of digestibility coefficients, therefore, is not necessarily the only factor involved in the animal's adjustment to a new diet. It is difficult to say if the final consumption levels for each diet (Table 10) represent the maximum values that would be obtained if the trials had been continued. It seems unlikely, however, that consumption levels would rise much beyond the observed maximum levels for each deer and diet. Several incidents were observed where, after seemingly becoming adjusted to a new diet, a deer decreased its level of consumption.

Most digestibility studies are ultimately concerned with biotic productivity and the actual amount of food energy utilized by an animal per unit time. To calculate the amount of energy utilization occurring, it is necessary to know the consumption rate as well as the digestibility coefficients of the foods being tested. Ideally, trials investigating productivity should not be initiated until both of these parameters have stabilized. As these trials with ^{51}Cr show, the time required for stabilization varies with different foods and previous feeding history.

Comparison of Dry Matter Digestibility Coefficients for Various Foods

Two trials using different foods were conducted for each of 3 deer using 3 natural foods. In addition, 3 combination diets were tested, 1 in each deer (Figure 5). The combination diets consisted of 1:1 wet-weight mixtures of 2 natural foods.

The 3 natural foods proved each to be digested to nearly the same extent. The average dry matter digestibility coefficients for the aspen, grass, and sumac diets were 50.70, 49.42, and 54.17 per cent, respectively (Table 11). These were all below the average digestibility coefficient of 65.68 per cent for the standard diet (Table 11).

Digestibility data were calculated for the mixed diets as if no synergistic or antagonistic effects were present between the 2 foods used. The estimates were obtained by taking the digestibility values for each food item as derived separately and obtaining a weighted average (Table 11). As an example, the aspen-grass mixture for Deer II would be expected to have a dry matter digestibility coefficient of 53.70 per cent if there were no interacting effects present. This was obtained by multiplying the digestibility coefficient of aspen 51.54 per cent, measured in Deer II, by its dry weight proportion of 0.56 in the aspen-grass mixture, and adding this product to the product for grass in Deer II, that is 56.47 per cent times 0.44.

DIET

	Individual Foods			Combinations		
Deer	Sumac	Aspen	Grass	Aspen & Grass	Aspen & Sumac	Sumac & Grass
II		X	X	X		
III	X	X			X	
IV	X		X			X

Figure 5. Feeding scheme used in digestibility studies of several natural diets in 3 deer. Michigan State University, 1968.

Table 11. Digestibility data for 7 diets fed to 3 deer during evaluation of the ^{51}Cr technique. Michigan State University, 1968.

Diet	Deer	Grams consumed per hour*	Kcalories consumed per hour*	Per cent of consumed energy excreted as: Feces	Urine	Kcalories digestible energy obtained per hour*
Aspen leaves	II	2.77	14.08	51.50	2.68	6.83
	III	1.13	5.44	50.74	3.37	2.68
Mean		1.95	9.67	51.12	3.03	4.76
Grass clippings	II	2.32	10.76	41.39	1.21	6.31
	IV	1.63	7.57	58.96	***	3.11
Mean		1.98	9.17	50.18	1.21	4.71
Sumac inflor-	III	2.17	11.56	55.39	2.54	6.36
escences	IV	2.02	10.75	50.56	***	5.31
Mean		2.10	11.16	52.98	2.54	5.84
		Observed Expected				
Aspen(56%) & Grass(44%)	II	2.68 2.52	13.09	47.34	2.11	6.89
Aspen(44%) & Sumac(56%)	III	2.72 1.47	15.31	47.70	4.94	8.01
Sumac(59%) & Grass(41%)	IV	1.79 1.86	9.02	60.71	***	3.43
Standard pel-						
leted diet	II	3.35	14.92	34.07	2.95	9.84
	III	3.37	15.01	32.04	1.68	9.66
		3.36	14.97	33.06	2.32	9.75

* All values standardized to $kg^{0.75}$ body weight.

** Expected values assuming no synergistic or antagonistic effects present between the 2 foods.

*** Insufficient data.

Kcalories metabolizable energy obtained per hour*	Dry matter digestibility coefficient	Gross energy digestibility coefficient	Gross energy metabilizability coefficient
6.45	51.54	48.50	45.82
2.50	49.85	49.26	45.89
4.48	50.70	48.88	45.86
6.18	56.47	58.61	57.40
<3.11	42.37	41.04	<41.04
<4.65	49.42	49.83	<49.22
6.07	55.12	55.05	52.51
<5.31	53.12	49.44	<49.44
<5.69	54.17	52.25	<50.98

Observed	Expected	Observed	Expected		Observed	Expected
6.62	6.27	53.34	53.70	52.66	50.55	50.92
7.25	3.66	52.80	52.80	52.30	47.36	44.21
<3.54	***	39.59	48.77	39.29	<39.20	***
9.40		66.63		65.93	62.98	
9.44		64.73		64.36	62.86	
9.42		65.68		65.15	62.92	

The only great deviation from expected values in the mixed diets was in the much greater consumption level and therefore in the calories derived by Deer III from the aspen-sumac mixture as compared with the 2 ingredients fed individually. The dry matter digestibility coefficient for the grass-sumac mixture in Deer IV was lower than expected, indicating a possible antagonistic effect.

Evidently there are synergistic and antagonistic effects involved with the food combinations used in this work. Future digestive studies might include appraisals of the total natural diet of the deer as determined by prior studies. Accurate estimates of digestive parameters are not necessarily obtained merely by lumping the appropriate data for individual forages.

Energy Value of Several Diets to the Deer

The energy derived by deer from different foods can be ascertained by comparing the consumption rate and dry matter digestibility of the food with the caloric values of food, feces, and urine.

Of the 6 natural diets tested, none provided the deer with as much energy as the formulated standard diet (Table 11). Animals on that diet obtained above-maintenance levels of energy as evidenced by continual weight gain. Of the natural foods tested, sumac inflorescences evidently comprised the best source of energy. A mixture of sumac and

aspen also provided the deer with an excess of calories.

Periodic weighings of Deer III showed that this animal lost weight while on the aspen diet and gained weight while on the sumac and aspen-sumac diets. Although periodic weighings were not possible, Deer II neither appeared to lose nor to gain weight markedly during 16 days on the aspen or 17 days on the grass diet. These deer required (Table 11) approximately 6 kilocalories of metabolizable energy per kilogram to the 0.75 body weight per hour.

Autopsy Results

To ascertain the areas of principal nutrient absorption, several deer were sacrificed upon completion of digestion trials. At the time of death, these animals had been consuming a constant level of ^{51}Cr on the standard diet. Since ^{51}Cr is not absorbed in the digestive process, it becomes increasingly concentrated as foods are absorbed from the gut.

Samples of digesta were withdrawn from the rumen, reticulum, omasum, abomasum, and cecum and from points every 12 inches along the small and large intestines of Deer I and V. Three other deer autopsied for this purpose proved to have digesta too scanty to allow adequate sampling.

As indicated by an increase in ^{51}Cr concentration (count/minute/dry gram) (Table 12), the major absorption of nutrients from the digesta occurred in the distal 1/5 of the small intestine, in the cecum, and in the proximal 1/5

Table 12. Count per minute per dry gram of samples of digesta withdrawn from various areas of the gastrointestinal tracts of 2 deer sacrificed while consuming a ^{51}Cr labeled standard diet. Michigan State University.

	Deer	
	I*	V
c/m/g ingested food	40	44
Portions of digestive tract	c/m/g	c/m/g
Rumen	49	34
Reticulum	46	32
Omasum	50	39
Abomasum	33	25
Small Intestine**		
0-20%	11	†
21-40	20	†
41-60	31	19
61-80	43	31
81-100	43	64
Cecum	113	115
Large Intestine		
0-20%	92	93
21-40	97	100
41-60	107	103
61-80	90	97
81-100	103	105
Total lengths:		
Small intestine	56 feet	33 feet
Large intestine	27 feet	19 feet
Cecum	16 inches	***

*Chyme of the small intestine of this deer contained appreciable amounts of blood.

**Due to differences in intestinal lengths between the specimens the data are expressed as percentages of total length so as to enable ready comparison.

***Not measured

†Insignificant ^{51}Cr levels.

of the large intestine. ^{51}Cr concentrations lower than that of the ingested food occurred in the proximal segments of the tract and indicated a dilution, probably by digestive secretions. In addition, some error was undoubtedly introduced when withdrawing digesta samples from the proximal area of the small intestine. In this area where only limited amounts of digesta were present, mucosa and cells from the intestinal endothelium diluted ^{51}Cr concentrations beyond that which normally exists.

Amount of Digesta Entering Cecal Pouch

The cecum of the deer is primarily a blind pouch 12 to 18 inches long and located at the junction of the small and large intestine. ^{51}Cr concentrations of digesta samples withdrawn from this blind pouch and from the intestines showed that a large proportion of digesta enters this organ. Chyme from the small intestine which does not enter the cecal pouch flows directly into the large intestine (Table 12), diluting the materials which reenter the intestine from the pouch.

In Deer V, the isotope concentration in digesta samples withdrawn from the tract immediately preceding the cecum, from the cecum, and from immediately after the cecal juncture were 64, 115, and 93 c/m/g respectively. Since 93 c/m/g is the weighted average of 64 c/m/g and 115 c/m/g, then the proportion of chyme contributed by the small intestine and that contributed by the cecum is:

let x = that portion of a gram contributed to the 93 c/m/g chyme of the proximal large intestine directly by the small intestine.

let 1-x = that portion of the proximal large intestine 93 c/m/g/ chyme contributed by the cecum.

$$(64 \text{ c/m/g} \cdot x) + [115 \text{ c/m/g} \cdot (1-x)] = 93 \text{ c/m/g}$$

$x = 0.431$ grams
$1-x = 0.569$ grams

Thus in order to obtain a final average of 93 c/m/g, 0.431 grams of small intestinal chyme bearing 64 c/m/g must be mixed with 0.569 grams of 115 c/m/g cecal chyme. The 0.569 grams of cecal chyme represents a total of 0.569 grams times 115 c/m/g or 65.4 counts of ^{51}Cr. Since this material originated from the small intestine at a concentration of 64 c/m/g it represents $\frac{65.4 \text{ cts}}{64 \text{ c/m/g}}$ or 1.022 grams of original small intestinal material. Therefore for every 0.431 grams plus 1.022 grams or 1.453 grams leaving the small intestine $\frac{1.022}{1.453} \times 100$ or 70.34 per cent enters the blind pouch of the cecum. For Deer I, 85.98 per cent of the material leaving the small intestine entered the cecal pouch.

Absorption in the Small Intestine, Cecum, and Large Intestine

The proportion of ingested dry matter absorbed from the various areas of the gastrointestinal tract can be calculated by multiplying the amount of original dry matter entering the segment by the degree of absorption occurring there: In Deer

V the absorption occurring between the animals mouth and the distal end of the small intestine was $(1 - \frac{44 \text{ c/m/g}}{64 \text{ c/m/g}}) \times 100$ (Table 12) or 31.25 per cent. Thus 68.75 per cent of the original meal remained at the distal end of the small intestine. The cecum of this animal absorbed $(1 - \frac{64 \text{ c/m/g}}{115 \text{ c/m/g}}) \times 100$ or 44.35 per cent of the dry matter which entered it. However, as previously discussed only 70.34 per cent of the dry matter leaving the small intestine entered the blind pouch of the cecum. Because only 68.75 per cent of the original meal reached the distal end of the small intestine and 70.34 per cent of this actually entered the cecal pouch then 68.75 per cent times 70.34 per cent or 48.36 per cent of the original meal entered the cecum. Since the material entering this organ was absorbed 44.35 per cent then 44.35 per cent times 48.36 per cent or 21.45 per cent of the original meal was absorbed in the cecal pouch of this deer.

The large intestine absorbed $(1 - \frac{93 \text{ c/m/g}}{105 \text{ c/m/g}}) \times 100$ (Table 12) or 11.43 per cent of the chyme which entered it. At the distal end of the cecum only 100 minus 31.25 less 21.45 or 47.30 per cent of the original meal remained. Since this was absorbed to an extent of 11.43 per cent then 11.43 per cent times 47.30 per cent or 5.41 per cent of the original meal was absorbed by the large intestine.

The total amount of material absorbed by Deer V was therefore 31.25 per cent from the mouth to the cecum, plus 21.45 per cent from the cecum, plus 5.41 per cent from the

large intestine or 58.11 per cent. This agrees with the figure arrived at by comparing the initial and final ^{51}Cr concentrations, that is, $(1 - \frac{44 \text{ c/m/g}}{105 \text{ c/m/g}}) \times 100$ or 58.11 per cent. The proportions of the total absorption contributed by the small intestine, cecum, and large intestine are 53.78 per cent, 36.91 per cent, and 9.31 per cent respectively.

The small intestine, cecum, and large intestine of Deer I absorbed 6.98 per cent, 49.55 per cent, and 4.64 per cent of the dry matter consumed by this animal. The total dry matter absorption for this deer was 61.17 per cent. Thus the proportion of the total absorption contributed by each organ was 11.41 per cent, 81.00 per cent, and 7.59 per cent for the small intestine, cecum, and large intestine respectively. These results are presented in Table 13.

These calculations assume that all materials secreted into the alimentary canal in the various segments of the tract are absorbed prior to the distal end of the segment in which they appeared. This is not always the case and therefore the true dry matter digestibility for the various areas of the tract may be slightly higher or lower than that observed.

The rumen and small intestine are generally considered to be the primary areas where absorption occurs. While this was seen in Deer V (53.78 per cent of total), data from Deer I indicate the proximal areas of the tract played only a minor role in its absorption processes (11.41 per cent of the total).

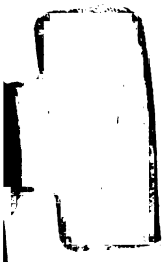


Table 13. Percentage absorption of food by portions of the digestive tract of 2 deer fed the standard pelleted ration. Michigan State University, 1968.

	As percentage of food entering organ	As percentage of total food absorbed
Deer I		
Small intestine	6.98	11.41
Cecum	49.55	81.00
Large intestine	4.64	7.59
Total	61.17	100.00
Deer V		
Small intestine	31.25	53.78
Cecum	21.45	36.91
Large intestine	5.41	9.31
Total	58.11	100.00

It seems unlikely that this could be the case in a healthy animal and there was in fact, evidence of ulceration of the gastrointestinal tract in Deer I. Chyme from several areas of the small intestine appeared very dark, as if there was much blood present. This disturbance could conceivably cause absorption to be decreased in this area of the tract. In addition, the blood entering the lumen of the intestine would dilute the ^{51}Cr of the chyme, thereby giving the appearance of low dry matter absorption in the small intestine. The absorption of much of this blood distal to the area of ulceration would also add to the appearance of increased cecal and large intestinal dry matter absorption. It is not known what caused this intestinal disorder. Due to malfunction of the counting device, rather large amounts of isotope were fed to Deer I. The total isotope ingested by this deer over a period of 67 days was 593 microcuries. Whether these levels of ^{51}Cr could cause the bleeding observed is not known.

In all events, this ^{51}Cr technique clearly discloses the importance of the cecum in the digestive process of white-tailed deer. Whether these findings also apply to natural diets of the deer remains for future study. It was unfortunate that data could not be obtained from 3 of the 5 deer used for these autopsy studies.

The above described technique of detecting where dry matter absorption occurs should also be of value in the

study of absorption of specific nutrients. By comparing individual nutrient concentrations with the ^{51}Cr indicator, values could be obtained regarding the site of absorption of specific ingredients of a diet. This particular ratio technique of studying absorption has been used for many years with stable indicators such as Cr_2O_3, but the use of ^{51}Cr simplifies indicator detection and makes possible the easier analysis of many samples.

Behavior of Experimental Animals

Emotional stress induced by confinement in some animals introduced a source of variation into experimental results which may not occur in wild populations. Collection-pen data from the more relaxed animals probably provided data which were more typical of wild deer than did results from excited test animals.

Deer I and II seemed to accept captivity. They seldom showed fear or apprehension and were the best suited of all deer used. Only after periods of 3 to 4 months in the collection pens did these animals show unrest. They would then occasionally hit and scrape the grated floor with their hooves. Even though raised as a fawn in captivity, Deer III constantly displayed an apprehensive behavior. Deer IV displayed similar behavior.

SUMMARY

Evaluation of ^{51}Cr as a Food Label in Digestive Studies with Deer

In the white-tailed deer ^{51}Cr proved to be a useful indicator for the study of many digestive parameters, particularly those involving passage rate, rumen turnover time, and the area of the tract where major nutrient absorption occurs. These are all areas of study which require some type of food label. The radioisotope ^{51}Cr has an advantage over stable indicators in its simple detection and quantification.

When ^{51}Cr was sprayed on all foods ingested, the degree of total digestibility could be determined by comparing the isotope concentration of the food with that of a few radioactive defecations. The ingestion of only a limited number of ^{51}Cr labeled food items, mixed thoroughly with nonlabeled food, however, yielded variable fecal isotope concentrations in the deer which necessitated lumping values from several defecations. When this must be done, there is little advantage of the ^{51}Cr ratio method over the total collection method. Consequently, the method requires that all food or at least a high number of individual food items be marked with ^{51}Cr.

The real advantage of the ^{51}Cr ratio method will be in digestibility studies on animals which do not allow severe confinement, thus making the total collection of feces impossible. For studies such as these the effort and time required for spraying all foods ingested with ^{51}Cr or labeling many individual food items easily will be justifiable. When this is done it will be possible to obtain digestibility coefficients by collecting just a few fecal samples.

There are also certain types of digestibility studies made on confined animals which are not possible with the total collection technique. The ^{51}Cr ratio method enables calculation of short term changes in digestibility occurring as results of stress, new diet, or other disturbances to the test animal.

Digestive Parameters of Deer Investigated with ^{51}Cr

The rumen was the major organ of the deer in which food mixing occurred but significant mixing of digesta also occurred in other areas of the tract. While feeding on a standard pelleted diet, ^{51}Cr placed on a 0.25 to 0.50 gram food pellet was thoroughly mixed with the rumen contents 5 to 30 minutes after ingestion. Rumen dry matter content varied greatly even within 1 animal consuming the standard diet. The mean rumen dry matter content for this animal (Deer III) was 547 grams.

There was an inverse relationship between food consumption level and passage rate. The relationship was variable, however, and it was not possible to use one parameter to predict the other.

A forced reduction of 23.62 per cent in dry matter intake had no effect on the digestibility coefficient of the standard diet even though the experimental animal studied was in a state of negative energy balance, losing 17 per cent of its body weight.

Two deer required 9 to 12 days to become adjusted to the collection pens in the amount of dry matter absorbed from the standard diet. Digestibility coefficients thereafter were the same as those observed when these specimens were confined to larger outdoor pens. One animal showed a permanent decrease in food consumption in the collection pen.

The 3 natural foods used in this study, aspen leaves, sumac inflorescences, and grass clippings, had rather similar dry matter digestibility coefficients (50.70, 54.17, and 49.42 per cent respectively). The standard pelleted deer diet had an average dry matter digestibility of 65.68 per cent. Of the natural foods tested, sumac inflorescences appeared to be the best source of energy for the deer. An animal which consumed only this food obtained above-maintenance levels of energy as did a deer consuming an aspen-sumac mixture. Aspen and grass when fed individually yielded the deer near maintenance levels of energy.

The small intestine, cecum, and large intestine of a deer consuming a standard ration accounted for 53.78, 36.91, and 9.31 per cent respectively of the total dry matter absorption occurring for this animal. For this deer 70.34 per cent of the material leaving the distal end of the small intestine entered the blind pouch of the cecum.

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