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DIGESTIBILITY OF COMMON FORAGE PLANTS
AND ENERGETIC REQUIREMENTS
OF THE BLACK-TAILED PRAIRIE DOG

by

Maureen A. Beckstead



A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science, Major in
Wildlife and Fisheries Sciences
South Dakota State University
1977

DIGESTIBILITY OF COMMON FORAGE PLANTS
AND ENERGETIC REQUIREMENTS
OF THE BLACK-TAILED PRAIRIE DOG

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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Date

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MAB

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ABSTRACT

Black-tailed prairie dogs (Cynomys ludovicianus) assimilated 51.5 percent of the wheatgrass (Agropyron intermedium) they consumed; thus, they would have to consume $0.148 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in order to obtain the $0.076 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ they would require to maintain their weight. Prairie dogs assimilated 31.5 percent of the buffalograss/blue grama mixture (Buchloe dactyloides/Bouteloua gracilis) they were fed. They would have to consume $0.229 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ of this forage to assimilate $0.072 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ and maintain their weight.

The proximate composition of forages fed in feeding trials was similar to that found for those collected on the study area. Total digestible nutrients (TDN) for wheatgrass in feeding trials and from the study site averaged 46.7 percent and 45.5 percent, respectively. The mean TDN for buffalograss/blue grama feeding trial and study area forages were 26.4 percent and 23 percent, respectively.

The assimilation efficiency (AE) of prairie dogs on their natural diet of 34 percent forbs and 65 percent grasses was 71.8 percent. The higher AE in the wild population than in captive animals fed grasses is due to the presence of highly digestible forbs.

The estimated Resting Metabolic Rate (RMR) of $0.056 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ is relatively low; 85 percent of the Basal Metabolic Rate as predicted by a metabolic body size formula. The energy cost of activity is the primary cause for the difference in RMR estimates from

oxygen consumption tests and caloric requirements found in feeding trials. The prairie dog feeding trial results were 1.32 times greater than the RMR estimates.

INTRODUCTION

The black-tailed prairie dog (Cynomys ludovicianus) is a colonial sciurid of the Great Plains prairies. Well-defined social behavior patterns lead to the establishment of dog towns (Koford 1958, King 1959, Smith 1967) and may result in concentrations that influence local plant succession (Smith 1967, Clark 1970, Bonham and Lerwick 1976).

The burrow system of prairie dogs provides refuges for other rodents, lagomorphs, burrowing owls (Speotyto cunicularia), black-footed ferrets (Mustela nigripes), badgers (Taxidea taxus), reptiles, amphibians and some insects (Koford 1958, King 1959, Smith 1967). Foraging and clipping by prairie dogs maintains a stage of plant succession favorable to pronghorn antelope (Antilocapra americana), lagomorphs, small seed-eating birds, grouse, ants and grasshoppers. Prairie dogs may form the bulk of the diet of snakes, hawks, eagles, coyotes (Canis latrans), foxes, badgers and the black-footed ferret in some areas (Koford 1958, King 1959, Smith 1967).

Prairie dog activities appear to increase the diversity of both perennial and annual plant species as well as the abundance of forbs and grazing-resistant grasses (Koford 1958, Clark 1970, Bonham and Lerwick 1976). Air and water penetration and mixing due to prairie dog activities benefit the soils in dog towns (Clark 1968). Soil is further improved by the addition of prairie dog urine, feces, carcasses and clipped plant parts (Koford 1958, Clark 1968).

Prairie dogs contribute to range deterioration by eating the basal

parts of some plants, digging for roots and eliminating vegetation in some areas (Koford 1958). Many investigators cited by Clark (1968) concluded, however, that concentrations of prairie dogs are the result of range deterioration rather than the cause. The expansion of prairie dog towns from 1968 to 1975 in the Conata Basin of the Buffalo Gap National Grasslands under season-long grazing systems was almost 11 times greater than that in the Badlands National Monument a few miles away where no livestock graze (U.S.D.A. 1977).

The prairie dog was the object of systematic eradication campaigns spanning almost 100 years. Nelson estimated that prairie dogs occupied more than 40.5 million hectares in the United States in 1919 (Summers 1975), but the total occupied area had been reduced to 567 thousand hectares by 1971 (Cain et al. 1972). It was suggested that the prairie dog would become extinct before its role in the grassland ecosystem could be determined (Longhurst 1944, Smith 1967). Prairie dog control by toxicants was banned on all public lands in 1972 by Executive Order 11643 (Federal Register 1972). Conflicts with livestock grazing are developing again in some areas and a proposal for management of prairie dogs by toxicants is currently being considered (U.S.D.A. 1977).

The animal damage problem is agriculturally, economically and biologically complex. There is particularly a lack of knowledge of prairie dog energetics. It is necessary to understand not only what an animal eats and how much, but what foods it has access to, seasonal variation in forage quality and physiological utilization of available nutrients.

The objectives of this study were: to determine the digestibility of important forage species; to find the assimilation efficiency of the black-tailed prairie dog; to delineate the chemical composition of important forage species and their nutritive quality; and to estimate the energetic requirements of the prairie dog from the above parameters. This study is part of a broader, long-term project to determine the role of prairie dogs in the rangeland ecosystem, the effect of prairie dog competition with livestock, and methods of prairie dog density regulation.

STUDY AREA

The study area is a part of the Conata Basin in the East Half Buffalo Gap National Grasslands. The study area encompasses about 155 square kilometers between the Badlands National Monument and the Pine Ridge Indian Reservation in southwestern South Dakota.

The U.S. Forest Service, Nebraska National Forest, is responsible for the administration of the Buffalo Gap National Grasslands. These grasslands are divided geographically and administratively into two districts, the Wall District and the Fall River District. The Wall District (East Half Buffalo Gap National Grasslands) is located in parts of Jackson, Pennington and Custer Counties, South Dakota. Government ownership comprises about half the total land area within the boundaries of the Wall District. This unit contains 15 grazing allotments with 31,219 ha of usable range. There are 4,843 ha of prairie dog towns, 15.5 percent of the usable range, which makes this the most concentrated area for prairie dogs in the United States (U.S.D.A. 1977). The Conata Basin study area contains six of the 15 allotments in the unit with 4,012 ha of prairie dog towns as of fall 1975 (U.S.D.A. 1977).

The study area is south of eroded badlands and contains soils from soft silty to clayey to thin clayey types (Westin et al. 1967). The land is nearly level and almost entirely rangeland. The natural vegetation is primarily wheatgrasses (Agropyron spp.), blue grama and buffalograss (U.S.D.A. 1976). Climatological data is collected at South Dakota State University Experiment Station near Cottonwood,

24 km from the study area. The average annual precipitation is 38 cm, of which 79 percent falls between April and September. The temperature ranges from 38 C or above in summer to -29 C or lower in winter, with an average annual temperature of 8.4 C. The growing season averages 126 days (Spuhler et al. 1968).

MATERIALS AND METHODS

The study was divided into four phases. First, feeding trials were conducted with major forage species to determine consumption, digestibility, assimilation efficiency of the prairie dog and the physiological utilization of the available nutrients. Second, forage from the study area was collected and analyzed to determine its nutritional quality and to compare it to the diet of captive animals in feeding trials. Third, stomach and fecal samples were taken from animals collected on the study area. These were analyzed and an assimilation efficiency determined to compare with that estimated from the feeding trials. Fourth, Resting Metabolic Rate (RMR) was determined through oxygen consumption tests as a check on the estimates from feeding trial data.

Feeding Trials

Prairie dogs are opportunists in the sense that their diet varies with plant abundance, colony location and season. Kelso (1939) in Montana, Koford (1958) in Colorado and Smith (1967) in Kansas found that various grasses composed two-thirds to three-fourths of the summer diet. King concluded forbs were the principle summer food in his study area in South Dakota (Koford 1958). Prairie dogs consumed 65 percent grasses, 34 percent forbs and less than 5 percent seeds and insects in the Conata Basin (Summers 1975). The same seven plant species were important both spring and summer and of these only buffalograss was not selected for in greater quantities than occurred

in the associated range survey. On an annual basis, western wheatgrass (Agropyron smithii), blue grama and buffalograss formed 48 percent of the diet, and scarlet globemallow (Sphaeralcea coccinea) contributed another 18 percent. Prickly pear (Opuntia polyantha), indianwheat (Plantago spp.) and threadleaf sedge (Carex filifolia) were seasonally important, but each formed less than 10 percent of the annual diet (Summers 1975).

Western wheatgrass and a combination forage of buffalograss and blue grama were selected as major species for the forage feeding trials. The digestibility of major forage species and assimilation efficiency (AE) of the black-tailed prairie dog were determined for this study in several series of caged feeding trials.

Fifteen adults and three young were captured from three sites on the study area (Fig. 1). In addition, seven adults and four young, originally from Conata Basin stock, were captured from a fenced colony near the Wildlife Research Farm, South Dakota State University, Brookings.

Captured prairie dogs were maintained indoors at the Wildlife Research Farm laboratory in groups of three or four to a cage. The animals were under artificial lighting which was timed to approximate the natural cycle. The basic laboratory diet consisted of alfalfa pellets, dried corn, carrots and potatoes, and fresh grass when available.

Western wheatgrass was not available locally in sufficient quantities for forage feeding trials. Intermediate wheatgrass was substituted since the proximate composition of the two species are similar. Percent crude protein and ether extract vary by 0.1 percent

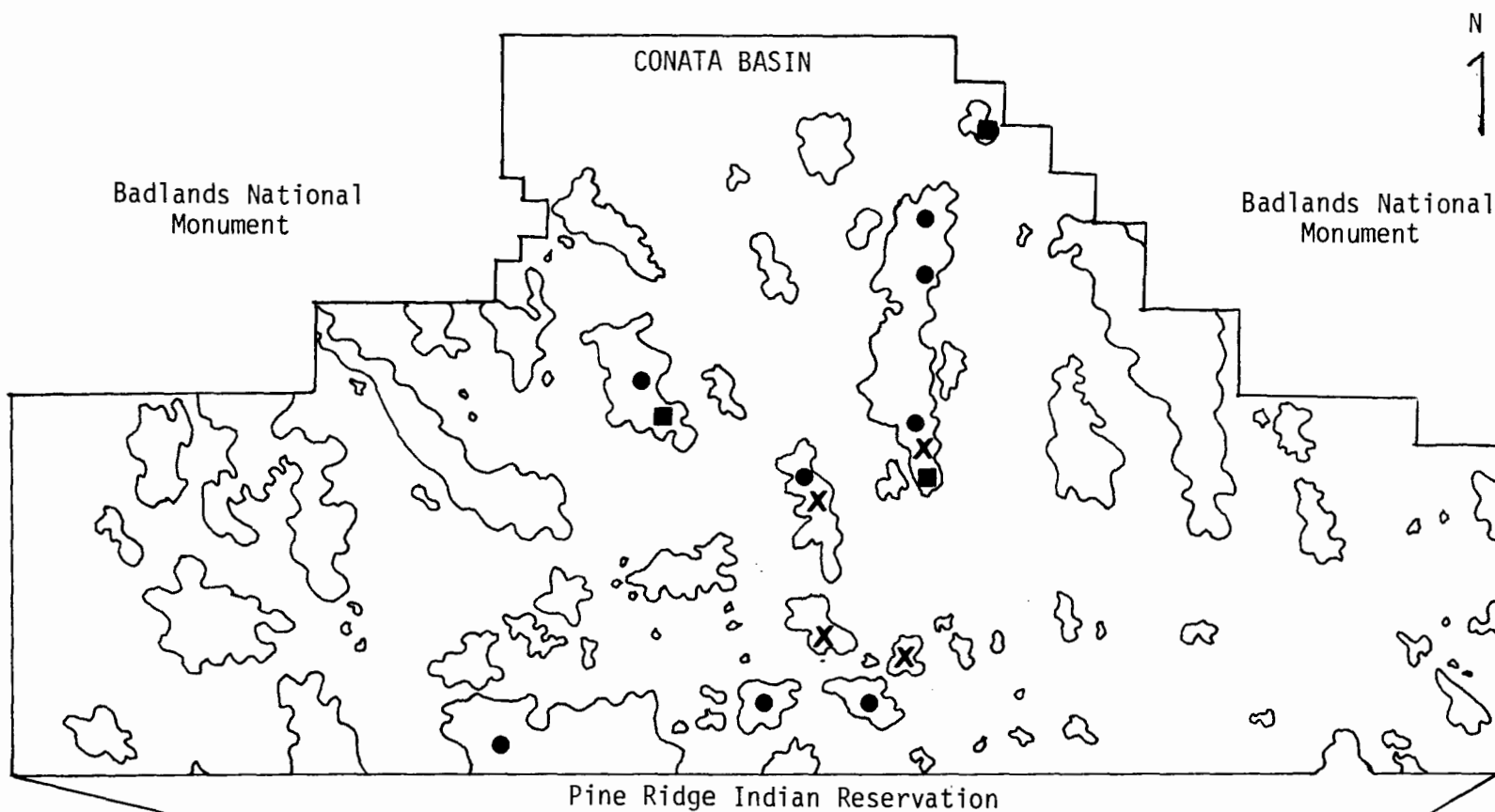



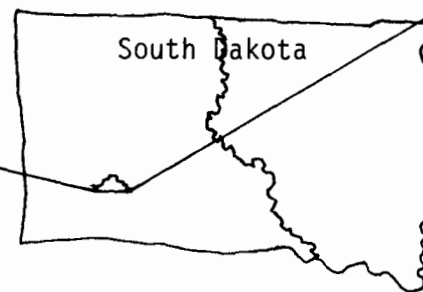
Fig. 1. Conata Basin collection sites

x = forage samples

● = GI tracts

■ = live capture

 = prairie dog colonies, 1975



and percent crude fiber, ash and nitrogen-free extract (NFE) vary by less than 5 percent between the two species (Miller 1958).

Three trials of four animals each were run between 26 June and 4 August 1976. Wheatgrass was cut daily and the seed heads removed and discarded. Prairie dogs were placed in individual metabolism cages for the feeding trials. These cages were large enough to allow some movement and free access to food and water. Three days of acclimatization to forage were followed by a day of fasting to clear the gastrointestinal (GI) tract. Each day, for five days, a pre-weighed amount of wheatgrass was offered. Twenty-four hours later all feces, urine and uneaten forage were collected from each individual. Animals were weighed the first day of trial and 24 hours after the last feeding. The same procedures were followed for two feeding trials of six animals each on a buffalograss/blue grama forage between 26 August and 12 September 1976.

Samples of the forage offered were oven dried to constant weight to determine moisture content. Feces and uneaten forage were also dried to a constant weight by evaporation for 36 to 48 hours at 60 C. Urine was measured by volume and weight and stored under refrigeration. Samples from the third and fifth trial days of each individual were ground on a 40 mesh screen with a Wiley Mill and sent to Iowa Testing Laboratories, Inc., for proximate analysis and acid-detergent fiber (ADF) tests. Laboratory results delineated percent protein, ether extract (fat), crude fiber, moisture remaining, ash (minerals), NFE (starches and sugars), carbohydrate (crude fiber + NFE), and ADF. Data for carbohydrates are not presented

in tables since they are simply a summation of crude fiber and NFE. The proximate analysis of crude fiber loses lignin and some other cell wall constituents to the NFE fraction, biasing both nutrient values (Kamstra, L. D. South Dakota State University, Brookings, pers. comm.). The ADF tests will be used in discussion in place of crude fiber since they provide a more accurate analysis.

Utilizing the proximate analysis figures, coefficients of digestibility were calculated for protein, crude fiber, NFE and ADF according to Kamstra (1975):

$$\text{Digestion coefficient} = \text{Digested} \cdot 100 / \text{Consumed} \quad (1)$$

Coefficients of digestibility for ash and fat were not calculated. Animals were assumed to be in mineral balance, in which case all ash ingested would be excreted eventually in feces and urine. The calculated ash not absorbed during digestion, y_n , was assumed to be excreted in the urine. Ash present in the feces often exceeds that ingested since it represents minerals that have been used by the body and then excreted into the gut at various rates. For the purposes of this paper, the digestion coefficient of fat will be assumed to be 1, indicating that it is completely digested. The actual value is impossible to calculate since both the metabolic processes of microflora and sloughing of the surface of the colon add lipids to the feces. Therefore, when only small amounts of fat are eaten, the feces may contain more fat than was ingested (Kamstra, pers. comm).

Total digestible nutrients were calculated using the digestion coefficients (Kamstra 1975):

$$\begin{aligned}
 & (\% \text{ protein})(d.c._p) + (\% \text{ fat})(d.c._f)(2.25) + \\
 & (\% \text{ crude fiber})(d.c._{cf}) + (\% \text{ NFE})(d.c._{nfe})
 \end{aligned} \tag{2}$$

where $d.c._p$ is the digestion coefficient of protein, $d.c._f$ is the digestion coefficient of fat, $d.c._{cf}$ is the digestion coefficient of crude fiber and $d.c._{nfe}$ is the digestion coefficient of NFE. Percent fat is weighted by a factor of 2.25 because of its relative caloric importance.

Assimilation efficiency was determined for each individual using the methods of Sohlt (1973):

$$AE = I - F / I \tag{3}$$

where I is the ash-free weight of the feed eaten and F is the ash-free weight of the feces. A Student's t test was applied to check for significant differences in AEs found between the first and last wheatgrass feeding trials (Steel and Torrie 1960).

The proportion of ash not absorbed, y_n , was calculated as a correction factor (Sohlt 1973) for use in the ash-tracer technique (Johnson and Maxell 1966, Johnson and Groepper 1970):

$$y_n = 1 - a_i - a_o / a_i \tag{4}$$

where a_i is the amount of ash ingested and a_o is the ash egested.

Forage Analysis

Samples of major forage species were collected from several sites (Fig. 1) in June and August 1975, as a part of a range evaluation by the Rocky Mountain Forest and Range Experiment Station, U.S. Forest Service. Separate collections in June and August were analyzed to determine the effect of maturation on nutritional quality as well as

the differences in cool and warm season grasses.

Samples of western wheatgrass and a combination of buffalograss/blue grama were selected for proximate analysis and ADF tests. Plots were clipped, sorted by species, and dried to a constant weight. The plants were ground to pass a 40 mesh screen and sent for testing to Iowa Testing Laboratory, Inc. Laboratory results reported the same series of nutrients as described for the feeding trial material; TDN was also calculated using digestion coefficients determined in feeding trials.

Assimilation Efficiency of Wild Population

Twenty-five adult prairie dogs were collected both in May and September 1976 (Fig. 1). Only six were collected in January 1977 due to poor weather conditions which kept prairie dogs below ground. Individuals were sexed, measured and checked for parasites; their GI tracts were removed and frozen. Records were kept on site, date and time of collection and weather conditions.

The assimilation efficiency of prairie dogs on their natural, composite diet was determined using the ash-tracer technique (Johnson and Maxell 1966, Johnson and Groepper 1970). Stomach contents and formed fecal pellets were individually washed, dried to a constant weight at 60 C for 48 hours, weighed and ground through a 40 mesh screen. Samples of approximately one g were ignited in a muffle furnace for three hours at 600 C and reweighed. An AE was then calculated using the y_n correction factor for ash not absorbed during digestion (Soholt 1973).

$$AE = 1 - (1/y)^{-1} / (1/y_0 y_n)^{-1} \quad (5)$$

where y is the fraction of ash in the feces, y_0 is the fraction of ash in the food source and y_n is the fraction of ash not absorbed during digestion. A Student's t test was employed to check for significant differences between the AEs found for May and September samples (Steel and Torrie 1960). Ash loss in the urine was considered to be the difference between ash ingested and that egested when the animals are in mineral balance.

Oxygen Consumption

Resting Metabolic Rate was measured on 18 adult prairie dogs while the animals were in a quiet, but not post-absorptive state, at temperatures believed to be within their thermoneutral zone. The RMR, therefore, included the Basal Metabolic Rate (BMR) plus the costs of specific dynamic action, but did not involve costs for thermoregulation. RMR was selected rather than BMR since it represented a more ecologically realistic measurement; BMR is not valid for animals which are growing, assimilating, active, reproducing or regulating their body temperature.

The RMR was determined with a paramagnetic oxygen analyzer in a negative pressure, open system. A vacuum pump pulled air through the system at 1000 ml per minute; air was dried in a tube of CaSO_4 before passing into the analyzer. Metabolic chambers were placed in an environmental chamber. Temperatures in the metabolic chamber and of the air before entry into the analyzer were measured with a multichannel telethermometer and automatically recorded along with percent oxygen from the analyzer on a chart recorder.

Metabolic chambers were constructed of 25.4 X 35.6 cm polyvinylchloride pipe with air entry at one end and exit at the other. The predicted lower critical temperature was calculated to be 13.5 C for these animals so the RMRs were measured at temperatures ranging between 21.5 and 27.0 C (mean 23.7C) to insure they were within their thermoneutral zone. Two animals in separate, darkened metabolic chambers were run at the same time. Weights were taken immediately before testing. A minimum of one hour was allowed for acclimitization after the chambers were connected to the air supply; no food or water was provided during testing. Calculations of oxygen consumption were made by difference between the percent oxygen supplied the animals and the residual oxygen concentration passing the analyzer. Data was collected when the recorder showed a minimum of two 10 to 15 minute readings maintaining the same oxygen concentration. All data was corrected to standard temperature and pressure.

RESULTS AND DISCUSSION

Feeding Trials

Twelve adult prairie dogs fed a wheatgrass diet consumed an average of 27.6 g of forage per day, dry weight, and excreted an average of 13.8 g of feces per day. Water consumption averaged 46.9 ml and mean urine production was 20.9 ml (Table 1). Both water and urine data were highly variable, apparently due to behavioral differences, so further analysis was not undertaken. The animals lost an average of 2.5 g body weight per day on this diet.

Prairie dogs digested an average of 55.4 kcal per day of wheatgrass, assuming the caloric value of mature wheatgrass to be 4 kcal per g, and metabolized 23.3 kcal of their own body fat. A maintenance diet of wheatgrass for animals averaging 1032 g would be 78.7 digestible kcal per day or $0.076 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. These figures correspond with the predictive formula (BMR) of Kleiber (1961): 71.7 kcal per day or $0.069 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. The maintenance diet is understandably higher than the BMR estimate due to the additional costs of activity, stress and specific dynamic action among the trial animals.

Twelve prairie dogs were fed a diet consisting of 79 percent buffalograss and 21 percent blue grama; data from one individual was discarded because the animal refused to eat. The mean forage consumption of the 11 remaining subjects was 10.1 g per day and the average fecal excretion was 6.9 g per day. Water consumption and urine production averaged 32.9 and 13.5 ml, respectively, and again were

Table 1. Results of wheatgrass (Agropyron intermedium) feeding trials, four individuals in each five-day trial.

	Trial I		Trial II		Trial III		Total Mean	
	\bar{x}	\bar{s}	\bar{x}	\bar{s}	\bar{x}	\bar{s}	\bar{x}	\bar{s}
Consumption/day (g) ^a	28.1	2.74	30.9	4.79	23.9	2.38	27.6	2.01
Feces/day (g)	13.2	1.69	15.9	2.66	12.3	1.35	13.8	1.13
Water/day (ml)	no data		59.4 ^b		34.4		46.9	9.73
Urine/day (ml)	44.1		15.1		3.7		20.9	6.72
Weight change/day (g) +4			-2.5		-9		-2.5	1.29

^aforage and feces dry weight

^bwater and urine total means highly variable; no further analysis undertaken

highly variable. The mean weight loss per day was 7.4 g (Table 2).

An average of 13.1 kcal of buffalograss/blue grama was digested per day and the animals metabolized 68.8 kcal from their own body fat. A total of 81.9 digestible kcal would be necessary to maintain prairie dogs averaging 1138 g or $0.072 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. The BMR formula predicts 77.1 kcal per day or $0.068 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$.

Results of the proximate analysis and acid-detergent fiber tests are presented in terms of the percent of each nutrient in the forage or feces as well as the amount, dry weight, of each nutrient consumed or excreted (Tables 3 through 6). The proximate composition of both forages was comparable to published values (Miller 1958). The largest variance was a 10 percent difference in NFE in western wheatgrass. The proximate composition of intermediate wheatgrass two weeks after heading was higher in protein, crude fiber, ADF and NFE than the feeding trial forages (Wurster et al. 1971).

The percent protein in the wheatgrass consumed was 9.6 as opposed to only 5.3 percent in the buffalograss/blue grama mixture. The percent protein in both forages dropped over the trials with increasing maturity. This increase in maturity was also reflected in the rise of percent ADF over the wheatgrass trials from 30.7 to 34.5 percent. Changes over time for the buffalograss/blue grama forage were not as apparent since both forages were past maturity when fed. A decrease in protein from 16 to 11 percent and an increase in ADF from 36 to 43 percent has been reported (Wurster et al. 1971) for intermediate wheatgrass over a two week period after heading. Similar changes in

Table 2. Results of buffalograss/blue grama (Buchloe dactyloides/Bouteloua gracilis) five-day feeding trials, five individuals in Trial I and six in Trial II.

	Trial I		Trial II		Total Mean	
	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$
Consumption/day (g) ^a	9.2	1.62	11.1	1.92	10.1	1.25
Feces/day (g)	6.6	1.16	7.1	1.26	6.9	0.82
Water/day (ml)	42.3 ^b		23.5		32.9	10.91
Urine/day (ml)	21.9		5.2		13.5	7.62
Weight change/day (g)	-8.8		-6		-7.4	1.23

^aforage and feces dry weight

^bwater and urine total means highly variable; no further analysis undertaken

Table 3. Mean nutrients (%) consumed and excreted during five-day wheatgrass (Agropyron intermedium) feeding trials, four individuals per trial.

	Trial I		Trial II		Trial III		Total Mean	
	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$
Protein:								
Forage	10.6	0.57	10.2	0.14	7.9	0.22	9.5	0.81
Feces	9	0.32	8.3	0.51	8.1	0.3	8.5	0.28
Fat:								
Forage	2.1	0.17	2.8	0.22	2.7	0.33	2.5	0.22
Feces	5.7	0.3	7.5	0.69	7.2	0.74	6.8	0.56
Crude Fiber:								
Forage	26.4	0.39	27.7	0.22	30.5	1.05	28.2	1.23
Feces	28.8	0.42	29.1	0.93	31.5	0.62	29.8	0.85
Ash:								
Forage	6.7	0.36	6.8	0	5.4	0.22	6.3	0.44
Feces	9.7	0.36	8.4	0.35	8.2	0.25	8.8	0.48
NFE:								
Forage	37.8	0.85	37	0.25	38.9	0.73	37.9	0.56
Feces	31.5	0.8	31.6	0.41	31	0.33	31.4	0.17
ADF:								
Forage	30.7	0.48	31.7	0.2	34.5	0.42	32.3	1.14
Feces	38.2	0.39	39	0.57	40.3	0.32	39.2	0.6

Table 4. Mean nutrients (%) consumed and excreted during buffalograss/blue grama (Buchloe dactyloides/Bouteloua gracilis) five-day feeding trials, five individuals in Trial I and six in Trial II.

	Trial I		Trial II		Total Mean	
	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$	\bar{x}	$s_{\bar{x}}$
Protein:						
Forage	5.5	0.1	5.1	0.1	5.3	0.17
Feces	6.4	0.14	6.2	0.35	6.3	0.1
Fat:						
Forage	1.2	0.14	1.1	0.1	1.2	0.1
Feces	1.8	0.17	1.6	0.1	1.7	0.1
Crude Fiber:						
Forage	25.6	0.26	24.7	0.35	25.2	0.46
Feces	26.1	0.58	26.6	0.25	26.3	0.28
Ash:						
Forage	9.2	0.2	9.4	0	9.3	0.14
Feces	9.1	0.17	8.4	0.6	8.8	0.33
NFE:						
Forage	44.6	0.35	44.9	0.91	44.8	0.1
Feces	42.7	0.68	42.8	0.33	42.7	0
ADF:						
Forage	34.5	0.17	34.5	0.25	34.5	0.1
Feces	36	0.46	36	0.37	36	0

Table 5. Mean nutrients (g dry weight) consumed and excreted during five-day wheatgrass (Agropyron intermedium) feeding trials, four individuals per trial.

	Trial I		Trial II		Trial III		Total Mean	
	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$
Protein:								
Forage	2.9	0.17	3.1	0.46	1.9	0.2	2.7	0.39
Feces	1.2	0.1	1.3	0.14	1	0.14	1.2	0.1
Fat:								
Forage	0.6	0	0.9	0.17	0.6	0.1	0.7	0.1
Feces	0.8	0.1	1.1	0.14	0.9	0	0.9	0.1
Crude Fiber:								
Forage	7.5	0.78	8.6	1.35	7.3	0.75	7.8	0.4
Feces	3.8	0.49	4.7	0.88	3.9	0.48	4.1	0.26
Ash:								
Forage	1.7	0.14	2.1	0.33	1.3	0.1	1.7	0.25
Feces	1.3	0.2	1.4	0.26	1	0.1	1.2	0.1
NFE:								
Forage	10.8	1.12	11.4	1.77	9.3	1.01	10.5	0.63
Feces	4.1	0.45	5.1	0.89	3.8	0.39	4.3	0.37
ADF:								
Forage	8.7	0.97	9.8	1.57	8.2	0.81	8.9	0.48
Feces	5.1	0.66	6.2	1.12	5	0.54	5.4	0.41

Table 6. Mean nutrients (g dry weight) consumed and excreted during five-day buffalograss/blue grama (Buchloe dactyloides/Bouteloua gracilis) feeding trials, five individuals in Trial I and six in Trial II.

	Trial I		Trial II		Total Mean	
	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$
Protein:						
Forage	0.5	0.01	0.6	0.1	0.5	0
Feces	0.4	0.01	0.4	0.1	0.4	0
Fat:						
Forage	0.1	0	0.1	0	0.1	0
Feces	0.1	0	0.1	0	0.1	0
Crude Fiber:						
Forage	2.3	0.41	2.7	0.46	2.5	0.2
Feces	1.8	0.33	1.9	0.35	1.8	0.1
Ash:						
Forage	0.9	0.14	1.1	0.17	1	0.1
Feces	0.6	0.1	0.6	0.14	0.6	0
NFE:						
Forage	4.1	0.73	4.9	0.77	4.5	0.4
Feces	2.8	0.5	3	0.54	2.9	0.1
ADF:						
Forage	3.2	0.57	3.8	0.66	3.5	0.33
Feces	2.7	0.41	3.2	0.36	2.9	0.25

chemical composition of western wheatgrass have been reported (Kamstra et al. 1968). A drop in percent protein concomitant with a rise in fiber content directly influenced the digestibility of forage and the assimilation efficiency of the consumer (Maynard and Loosli 1969). Although prairie dogs consumed an average of 2.7 g of protein per day on a wheatgrass diet, only 0.5 g of protein were consumed per day on buffalograss/blue grama due to lower consumption and lower protein content. Digestible protein in wheatgrass forage was greater than 50 percent, but less than 20 percent in buffalograss/blue grama. A 1 kg animal needs 3.65 g of digestible protein per day (Brody 1945).

Digestion coefficients (1) and TDN (2) for all nutrients in the wheatgrass trial (Table 7) were closely comparable to those found in digestibility studies on wheatgrass fed lambs (Wurster et al. 1971). However, the digestion coefficients and TDN for buffalograss/blue grama appear quite low (Table 8). Total digestible nutrients, calculated from the digestion coefficients, was 46.7 percent in wheatgrass and 26.4 percent in buffalograss/blue grama. The low digestibility of both forages resulted in prairie dog assimilation efficiencies of 51.5 percent for wheatgrass and 31.5 percent for buffalograss/blue grama. The AE are quite low. Caecal animals on nutritious spring grasses may have an AE from 55 to 75 percent (Johnson and Maxell 1966, French et al. 1976). Maintenance consumption of western wheatgrass is $0.148 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ with an AE of 51.5 percent; buffalograss/blue grama maintenance consumption would be $0.229 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ assuming an AE of 31.5 percent. Food intake of juvenile prairie dogs weighing

Table 7. Forage total digestible nutrients (TDN)(%), assimilation efficiency (AE)(%) and digestion coefficients (%) calculated from wheatgrass (Agropyron intermedium) feeding trials, four individuals per trial.

	Trial I		Trial II		Trial III		Total Mean	
	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$	\bar{x}	$S_{\bar{x}}$
TDN	47.4	0.5	45.9	0.48	46.8	0.3	46.7	0.28
AE	54.9	1.89	49.9	1.42	49.6	1.69	51.5	1.15
<u>Digestion coefficients:</u>								
Protein	60.1	2.47	58.5	1.98	47.1	4.02	55.2	1.81
Crude Fiber	49.8	2.17	46.4	2.77	46.7	2.01	47.6	1.3
NFE	61.6	0.54	56.4	1.49	58.7	0.77	58.9	0.84
ADF	42.2	1.98	37.2	2.32	41.2	2.48	40.2	1.35

Table 8. Forage total digestible nutrients (TDN)(%), assimilation efficiency (AE)(%) and digestion coefficients (%) calculated from buffalograss/blue grama (Buchloe dactyloides/Bouteloua gracilis) feeding trials, five individuals in Trial I and six in Trial II.

	Trial I		Trial II		Total Mean	
	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$	\bar{x}	$\frac{s}{\bar{x}}$
TDN	24	0.4	28.8	0.49	26.4	0.81
AE	27.5	2.48	35.5	1.95	31.5	1.94
<u>Digestion coefficients:</u>						
Protein	16	1.59	23.7	3.25	19.8	2.45
Crude Fiber	26.1	1.27	31.1	2.3	28.6	2.1
NFE	30.7	2.24	39	2.32	34.8	2.02
ADF	24.2	4.32	34	2.43	29.1	2.95

625 to 1400 g is 0.07 to 0.21 kcal · g⁻¹ · day⁻¹ (Hansen and Cavender 1970). An extensive feeding trial was run on growing prairie dogs by Hansen and Cavender (1973) using a ration containing 16 percent protein, 2 percent fat and 22 percent fiber. I extrapolated their findings on consumption and digestion and compared them to my data (Table 9). Differences can be accounted for in the digestibility and nutritional quality of the rations offered. Prairie dogs on a diet of only mature western wheatgrass or buffalograss/blue grama would probably starve because of the low nutritive quality and low palatability of the grasses.

Forage Analysis

Wheatgrass and buffalograss/blue grama were collected in June and August 1975. Proximate analysis and ADF content were determined by an independent laboratory using the techniques of Horwitz (1975); TDN was calculated from digestion coefficients obtained in feeding trials (Table 10). The mean percentages of all nutrients analyzed for appeared quite similar to those of the forages fed in feeding trials. The nutrients varied by 2 to 4 percent or less in wheatgrass, and by less than 6 percent in the buffalograss/blue grama forage except for percent ash. The ash content in wheatgrass and buffalograss/blue grama from the study site was from 4 to 10 percent higher than that in the feeding trial forages. Much of this might result from surface soil blown onto the field grasses and found in the bottom of clipping bags.

The decrease in protein content and increase in ADF or crude fiber with maturity was similar to that found for feeding trial forages collected locally. The apparent increase in TDN from June to August

Table 9. Feeding trial results compared with data extrapolated from Hansen and Cavender's (1973) October feeding trial.

	<u>Agropyron intermedium</u>	<u>Buchloe dactyloides</u> <u>Bouteloua gracilis</u>	Hansen & Cavender
<u>Original mean weight (g)</u>	1032	1138	988
<u>Weight change/day (g)^a</u>	-2.5	-7.4	+0.2
<u>Assimilation efficiency</u>	51.5	31.5	79
<u>Maintenance digestion</u> <u>(dry weight)</u>			
g/day	19.7	20.5	18.3
g/g body weight/day	0.019	0.018	0.018
kcal/day ^b	78.7	81.9	80.3
kcal/g body weight/day	0.076	0.072	0.081
<u>Maintenance consumption</u> <u>(dry weight)</u>			
g/day	38.2	65.1	23.1
g/g body weight/day	0.037	0.057	0.023
kcal/day	152.8	260.3	101.7
kcal/g body weight/day	0.148	0.229	0.103

^aAll data adjusted for weight gain or loss using 9.3 kcal per g (Hansen and Reed 1969) as the caloric value of fat

^bCaloric equivalents of rations: 4 kcal per g in feeding trials; 4.4 kcal per g in Hansen and Cavender (1973)

Table 10. Mean nutrients (%) in forages collected on the study area and total digestible nutrients (TDN)(%) calculated from feeding trial digestion coefficients.

	<u>Agropyron smithii</u>				<u>Buchloe dactyloides/Bouteloua gracilis</u>			
	<u>June (n = 4)^a</u>		<u>August (n = 2)</u>		<u>June (n = 8)</u>		<u>August (n = 4)</u>	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
TDN	42.6	2.19	47.5	2.31	23.9	1.79	22	0.94
<u>Nutrients:</u>								
Protein	10.5	2.36	6.4	1.05	9.6	2.26	6.5	0.84
Fat	1.5	0.5	3.7	1.65	1.3	0.79	0.4	0.2
Crude Fiber	24.3	1.85	26.4	2.64	22.4	1.58	21.6	1.34
Ash	10.1	2.25	10.9	1.68	13.9	3.72	18.1	1.36
NFE	36.9	2.12	39.2	3.9	36.4	4.07	39.3	3.29
ADF	no data		38.7	0.31	35.1	1.5	40.4	0.86

^an = number of samples analyzed; June samples are individual meter-plots, August samples are composites of ten meter-plots

in wheatgrass was misleading. The TDN figure for the August clipping was biased upwards by the high reported fat content which, when multiplied by a factor of 2.25 and a digestion coefficient of 1, assumed a much greater importance than may be warranted.

It appeared, then, that extrapolation from laboratory feeding trials to field conditions was warranted in regard to the nutritional quality of the forage.

Assimilation Efficiency of Wild Population

Prairie dogs are opportunists in the Conata Basin where their diets consist of 65 percent grasses and 34 percent forbs (Summers 1975). Prairie dogs on this natural, composite diet had an AE of 71.8 percent (Table 11). The mean y_n , determined in feeding trials, for wheatgrass was 0.6960 and was 0.6473 for buffalograss/blue grama. An average correction factor of 0.6717 was used in the AE calculations.

Only two of the six animals collected in January contained material in the GI tract and the two stomach and fecal samples analyzed both contained large amounts of what appeared to be soil. Thus, the January samples were not used in the calculation of the mean. The September young were not included in the calculation of the mean since the sample size was small and none were collected in May. Johnson and Groepper (1970) concluded, however, that the ash-tracer technique would provide a good estimate of AE for juveniles since they ingest more minerals than their growth would demand, leaving them in mineral balance.

The difference in AE between May (72.9) and September (70.6) was not significant ($P > 0.05$). The decrease in AE of the laboratory

Table 11. Percent ash in stomach and fecal samples and assimilation efficiencies of prairie dogs (*Cynomys ludovicianus*) on a natural composite diet.

	<u>Percent Ash Stomachs</u>		<u>Percent Ash Feces</u>		<u>Assimilation Efficiency</u>	
	\bar{x}	SD	\bar{x}	SD	\bar{x}	SD
May (n = 24) ^a	7.8	1.38	17.3	2.75	72.9	5.76
September (n = 22)	6.4	2.38	13.8	3.5	70.6	11.17
Mean for May and September (n = 46)	7.2	2.02	15.6	3.58	71.8	8.75

^an = number of animals from which samples were taken

animals over the same period of time on a wheatgrass diet was twice that observed in the wild population. The difference between the first and third feeding trial AEs was significant ($P < 0.05$). The presence of forbs in the diet of wild prairie dogs is responsible for maintaining a more nutritious diet and higher AE. Grasses are more subject to a decreasing digestibility due to greater lignification and calcification of the plants with growth (Cook 1971).

The AE of 14 species of grazing herbivores (microtines) on natural foods was found by Grodzinski and Wunder to average 65 percent (French et al. 1976). Johnson and Groepper (1970) found the AE of three species of rodent grazers to range from 76.3 to 82.4 percent using the ash-tracer technique on stomach and fecal samples; ash not absorbed during digestion ranged from 50 to 61 percent of that ingested. The AE of pikas (Ochotona princeps), determined by the ash-tracer method, averaged 68 percent with a range from 54 to 76 percent (Johnson and Maxwell 1966).

Oxygen Consumption

The resting metabolic rate of prairie dogs was $0.056 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ (SD = 0.01) or 71.6 kcal per day (SD = 15) for animals averaging 1312 g. The range was broad; from 0.036 to $0.078 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ or 50.5 to 97.5 kcal per day (Fig. 2). Two individuals that were very active in the chambers at higher temperatures were not included in the calculation of the mean. The lower critical temperature for prairie dogs averaging 1312 g in body weight with a mean body temperature of 37.5 C was 13.5 C , according to a formula given in Morhardt and Gates

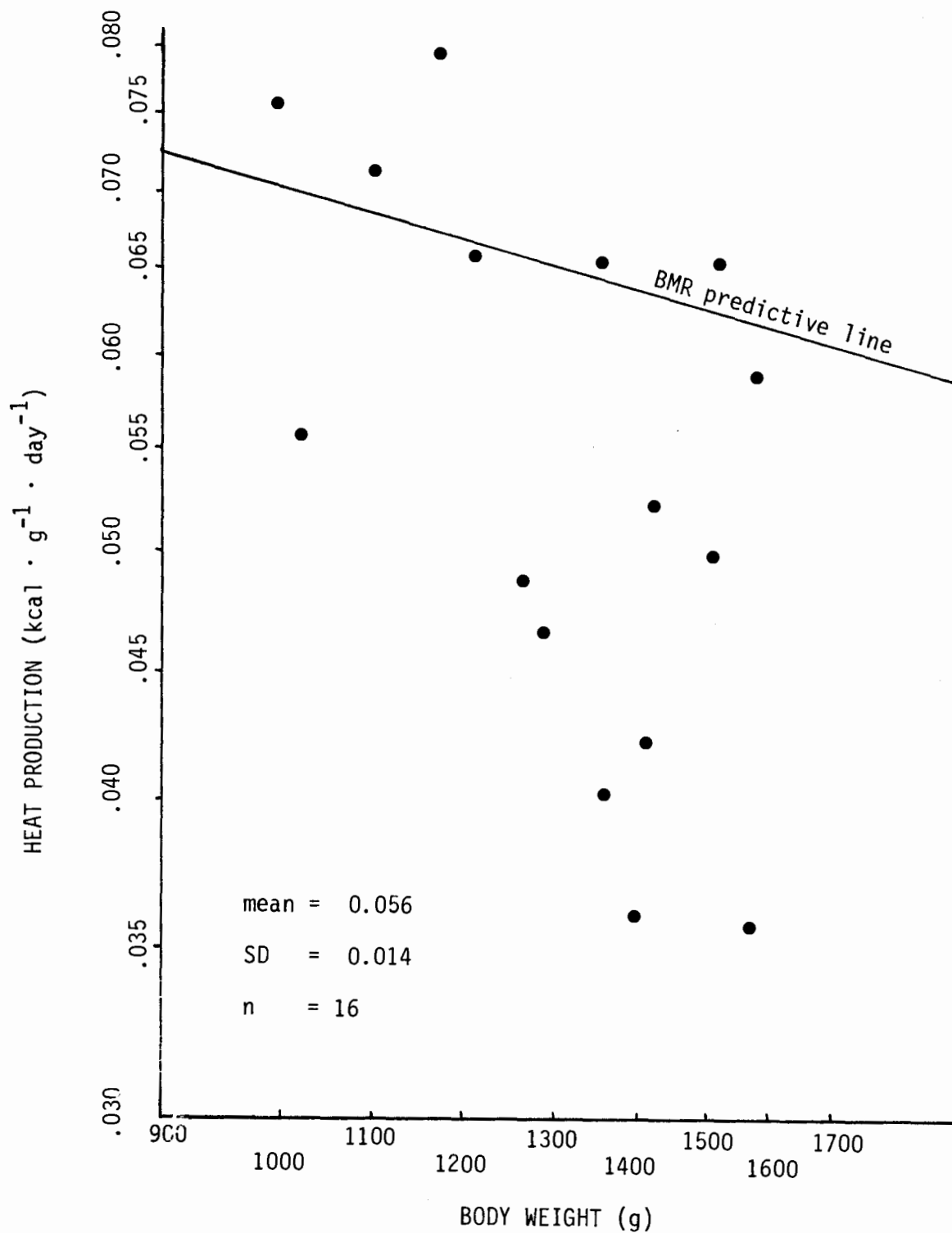


Fig. 2. Resting Metabolic Rate for prairie dogs (measured at temperatures between 22 and 25 C) plotted against body weight on a double-logarithmic grid.

(1974). Oxygen consumption was determined at temperatures between 22 C and 25 C, well within the thermoneutral zone of prairie dogs.

The mean RMR is only 85 percent of the predicted mean BMR (Kleiber 1961) of $0.066 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ or 85.7 kcal per day. Typically the RMR is estimated to exceed BMR by 15 percent (Brody 1945).

Physiological adaptation to an extreme environment and mode of existence may explain the low metabolic rate of prairie dogs. The prairie dog burrow system provides a damp microclimate, nearly constant in temperature (Koford 1958). Burrows provide protection from environmental extremes, but create physiological stresses also. Evaporative and convective cooling and the oxygen content of the air are all reduced in a burrow system (Baudinette 1972). Physiological adaptations to these conditions have been noted in several rodent species.

McNab (1966) found the metabolic rate of fossorial mammals to be from 40 to 90 percent of the predicted and that of mammals from arid environments to be 67 to 92 percent of the expected. The basal metabolic rate of Spermophilis beecheyi is 25 percent lower than the predicted value (Baudinette 1972). Hudson and Bartholomew concluded that small mammals from hot, dry areas have a reduced metabolic rate and a high thermoneutral zone as a means of entering torpor or estivation at temperatures within the usual thermoneutral zone (Baudinette 1972). McNab (1966) concluded that both fossorial rodents and mammals from arid environments conformed to environmental demands. A reduced metabolism in mammals from hot, dry areas means lower

respiratory exchange and less water loss. Fossorial rodents that have low metabolic rates have reduced heat production and storage.

A lower metabolic rate also results in a reduction in gas exchange which may prevent anoxia or acidosis from reduced oxygen in the burrow. Hall (1965) determined that, of seven species of sciurids studied, the prairie dog had blood that became 50 percent oxygen saturated at the lowest pressure. The prairie dog oxygen dissociation curve was shifted to the left, presumably as an adaptation to the reduced oxygen tension in their deep burrows (Hall 1965). One mechanism of achieving this shift to the left in the curve would be by a reduction in metabolic rate (Baudinette 1972). Prairie dogs may have adapted to their hot, arid, semi-fossorial existence by reducing their metabolism, thereby solving several physiological stresses at once.

The difference between the RMR found in oxygen consumption tests and caloric requirements determined in feeding trials (0.056 and 0.074 kcal \cdot g⁻¹ \cdot day⁻¹, respectively) may be explained by the difference in activity levels. Animals in the metabolic chambers were tested in the dark and measurements were taken only when activity was at a minimum or non-existent. Feeding trial animals were in cages large enough to allow freedom of movement, were engaged in feeding, and were subject to additional stress from the presence of personnel. The cost of activity is generally considered to be about 1.5 times the RMR (Grodzinski and Gorecki 1967). The prairie dogs in feeding trials had requirements 1.3 times the RMR estimated from oxygen consumption tests.

CONCLUSIONS

As forages mature, the drop in protein and increase in fiber content directly influences the digestibility of forages and assimilation efficiency of the prairie dog. Total digestible nutrients for wheatgrass over all trials averaged 46.7 percent. The prairie dogs' mean assimilation efficiency was 51.5 percent. The mean total digestible nutrients for buffalograss/blue grama were 26.4 percent and the assimilation efficiency on this diet averaged 31.5 percent. The assimilation efficiency of prairie dogs on their natural, composite diet of forbs and grasses averaged 71.8 percent.

Prairie dogs on a wheatgrass diet with an assimilation efficiency of 51.5 percent had to consume $0.148 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ in order to obtain the $0.076 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ they required to maintain their weight. Prairie dogs assimilated 31.5 percent of the buffalograss/blue grama mixture they were fed so had to consume $0.229 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ to digest the $0.072 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$ they needed.

The Resting Metabolic Rate of prairie dogs is $0.056 \text{ kcal} \cdot \text{g}^{-1} \cdot \text{day}^{-1}$. This value is only 85 percent of the predicted Basal Metabolic Rate. The difference between the Resting Metabolic Rate estimated from oxygen consumption tests and caloric requirements found in feeding trials may be explained by the difference in activity levels. The cost of activity is generally considered to be about 1.5 times the Resting Metabolic Rate; the prairie dog feeding trial results were 1.3 times greater than their Resting Metabolic Rate estimates.

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