1975

Some aspects of renal function temperature regulation and body weight changes in dehydrated black-tailed prairie dogs (Cynomys ludovicianus)

James Dennis Hamilton
The University of Montana

SOME ASPECTS OF RENAL FUNCTION, TEMPERATURE REGULATION,

AND BODY WEIGHT CHANGES IN DEHYDRATED BLACK-TAILED

PRAIRIE DOGS (<u>CYNOMYS</u> <u>LUDOVICIANUS</u>)

By

James D. Hamilton

B.A., St. Ambrose College, 1965

Presented in partial fulfillment of the requirements for the degree of
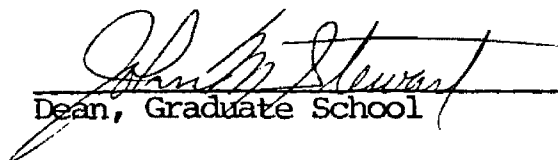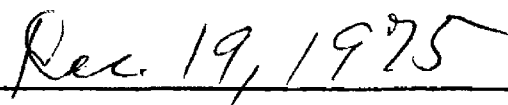

Master of Arts

University of Montana

1975

Approved by:

_____
Chairman, Board of Examiners

_____
Dean, Graduate School

_____
Date

UMI Number: EP37369

UMI

Dissertation Publishing

UMI EP37369

ProQuest

Hamilton, James D., M.A., December 1975   Zoology

Some Aspects of Renal Function, Temperature Regulation, and Body Weight

Changes in Dehydrated Black-Tailed Prairie Dogs (Cynomys ludovicianus) (44 pgs.)

Director: E. W. Pfeiffer

Black-tailed prairie dogs (Cynomys ludovicianus) were deprived of food and water for several days during the summer and for several weeks during the fall and winter. The summer experiments were carried out at room temperature and the winter experiments were carried out in a hibernaculum between 5-8° C. Abdominal temperatures were determined in some of the animals by radiotelemetry.

Summer dehydrated animals were killed when maximum urine concentration was achieved. Active winter dehydrated animals were killed after 7-35 days in the hibernaculum with Tb varying between 17-35° C. Torpid winter dehydrated animals were killed after 19-42 days in the hibernaculum when their body temperatures indicated they were in torpor.

Kidneys were removed immediately after death, a central section was cut out and frozen in dry ice and acetone, and slices of cortex and medulla were analyzed for urea, sodium, and potassium concentrations. Blood and terminal bladder urine were also obtained and urea, sodium, potassium, and osmotic concentrations were determined. Body weights were determined at the beginning and end of each experiment.

The data show that summer dehydrated prairie dogs lost weight rapidly, reached a maximum urine concentration ceiling in 3-4 days or less, possessed a pronounced renal medullary solute concentration gradient and the highest plasma urea and osmotic concentrations observed in these experiments. Active winter dehydrated animals had a higher per day weight loss than torpid animals, and a pronounced renal medullary solute gradient (varying with T_b). Winter torpid animals lost less weight per day than other animals, did not possess a renal medullary solute gradient, had the lowest plasma urea and osmotic concentrations, and were not dehydrated at the termination of the experiment. The torpid animals displayed short, cyclical patterns of extreme changes in body temperature (in torpor, 8-11° C, in the active state, 32-36° C).

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

v

ACKNOWLEDGEMENTS

I wish to thank the chairman of my committee, Dr. E. W. Pfeiffer for his patience, critical advice, and needed assistance during the course of my research. I believe that I will have the distinction of being the only "Green Beret" to have had Dr. Pfeiffer as an advisor. Dr. Pfeiffer spent many hours revising the manuscript, and gave needed instruction in the proper method of preparing a thesis.

The late Dr. James R. Templeton was most instrumental in enabling me to pursue this graduate study and I will always be grateful to him for that opportunity. The encouragement and guidance shown by my committee members is greatly appreciated: Dr. Delbert Kilgore assisted me in obtaining the prairie dogs and constructed the body temperature recording apparatus; Dr. Gregory Patent provided valuable advice throughout the course of study; Dr. Howard Reinhardt gave professional advice on the statistical tests used in the study. Finally, I would like to thank Dr. George Weisel and Dr. Franklin Sogandares-Bernal for serving as interim members of my graduate committee.

Many other people gave me help during the course of this study and their assistance is greatly appreciated. Dr. Mark Behan donated a good portion of his time showing me the instrumentation involved in using the flame spectro-photometer. I also wish to thank William Morrelles, for his patience and help in devising the body temperature monitoring system; William Cowan and Robert Mayes for their diligence in housing and feeding the animals; Larry Reinking for his helpful advice, critical suggestions, and assistance in surgery; Dr. John Mitchell for his advice and assistance in the preparation of the manuscript; Major General John J. Womack for allowing me use of the prairie dogs on the Ft. Harrison Military Reservation; and finally to Capt. Michael Smith for his

vi

assistance in trapping, feeding, and housing of the animals.

I especially wish to thank my wife Katherine, who supported me through employment, understanding, and patience for the past three years. Without her unceasing support, I would never have been able to complete this research.

CHAPTER I

INTRODUCTION

During the past twenty five years, many investigators have studied the problems of physiological adaptation to extreme environments in homeothermic animals. A search through the literature indicates that much of this work involves the study of estivation and hibernation in mammals, most notably among members of the family Sciuridae. Hudson (1964) described estivation as the phenomenon of summer dormancy, which differs from hibernation on the basis of seasonality and temperature. Hibernation has been defined several ways, none of which seem satisfactory to all of the researchers in hibernation physiology. Hoffman's (1964) definition of hibernation, which still remains acceptable in view of the current research being done in this field, is described as a periodic phenomenon in which body temperature falls to a low level approximating the ambient temperature, with heart rate, metabolic rate and other physiologic functions falling to minimal levels.

Considering the obvious species variations in response to temperature changes, fasting, ease of entering hibernation and depth of hibernation, terminology has been proposed for several types of hibernation. Seasonal hibernators are those that adhere to a cyclical rhythm and enter hibernation regardless of ambient temperature (Ta) and/or food and water deprivation; this is the case with most sciurid hibernators. Conversely, obligate hibernators do not adhere to any cyclical rhythm in hibernating and are forced to hibernate (or become hypothermic) under certain conditions of food deprivation or reduced temperature, or both (Morrison, 1960). Morrison states that permissive hibernators store and use food prior to hibernation and during periods of arousal, thus appearing to have an option as to hibernation.

1

Folk (1966) believed that seasonal hibernation is spontaneous and starts prior to stress, whereas obligate hibernation is induced and is a result of stress. Examples of seasonal hibernators would be yellow-bellied marmots (_Marmota flaviventris_) and Columbian ground squirrels (_Spermophilus columbianus_). The Syrian hamster (_Mesocricetus auratus_) is an example of a permissive hibernator, and the pocket mouse (_Perognathus_ sp.) is a representative obligate hibernator.

In this study, I propose to divide hibernation into two categories: obligate and facultative. An obligate hibernator would be an animal that is required to hibernate (or become torpid) because of seasonality, temperature stress, food and/or water deprivation, etc. A facultative hibernator (or hypotherm) would not be required to become torpid if subjected to the aforementioned conditions, thereby having the option of remaining active (aroused) or lowering its body temperature (T_b) and remaining in a torpid state for a certain length of time. The black-tailed prairie dog (_Cynomys ludovicianus_) belongs to the family Sciuridae, but is not considered a "true hibernator" in the classical sense (seasonal type), whereas a closely related species, the white-tailed prairie dog (_Cynomys leucurus_) does hibernate during the winter and is considered a true seasonal hibernator. King (1955) writes "periods of winter dormancy and decreased activity have been observed in captive prairie dogs. Gunnison's prairie dog (_Cynomys gunnisoni_) went into hibernation for the winter, whereas _C_. _ludovicianus_ slept for short intervals of 3-4 days throughout the winter. Observations suggest that hibernation is less complete in _C_. _ludovicianus_ than in related species, with short periods of dormancy during the winter appearing to be characteristic. The animals apparently hole up during the worst weather, but come out at intervals when the weather is more favorable."

Literature dealing specifically with hibernation in the black-tailed prairie dog is meager. Anthony (1955) observed sporadic rather than continuous hibernation occurring with this species, as evidenced by the frequent appearance of prairie dogs above ground in the middle of the winter. In his laboratory colony of prairie dogs, Anthony was able to induce short periods of lethargy at very low ambient temperatures, provided that available food and water were removed from the animals. Three prairie dogs that Anthony kept in an outdoor cage during freezing temperatures up to 14 days, lost considerable weight and went into a much deeper dormant state which he referred to as a "cold narcosis". Tileston and Lechleitner (1966) compared the black-tailed and white-tailed prairie dogs in North-Central Colorado and dispute the evidence in support of the assumption that C. leucurus "hibernates" and C. ludovicianus does not hibernate. Their observations indicate that the total activity and food intake of C. ludovicianus is greatly reduced during the winter. Further, they observed that during early winter only portions of the C. ludovicianus population were active above ground at any one period. They felt that a portion of the black-tailed prairie dogs in a particular town may have become dormant in shifts, with some animals arousing periodically to come above ground for limited times and limited activities.

There have been few studies in the laboratory done with black-tailed prairie dogs during torpor. Using external thermocouples attached to the animal, J. Turner (Personal Communication) has found that C. ludovicianus is capable of lowering its body temperature to 5°C when the ambient temperature is 5°C (only between Oct-Feb). Turner also observed the activity of C. ludovicianus during torpor and found that the animal will arouse every 4-5 days to urinate and occasionally defecate (Ibid).

Whether or not C. ludovicianus hibernates or remains active throughout

the late fall-early spring is important when one considers the stressful environmental conditions experienced by this animal during this period. Black-tailed prairie dogs are largely dependent upon annual forbs and grasses for food (Tileston and Lechleitner, 1966). During the late fall, winter, and early spring, the black-tailed species frequently eat the roots of several varieties of forbs and grasses (Tileston and Lechleitner, 1966 and Smith, 1958). Black-tailed prairie dogs have not been observed to drink water in the wild (King, 1955), and drink very little water in the laboratory while in captivity (Boice and Witter, 1970). With the onset of winter, most of the moisture providing vegetation that $C.$ ludovicianus requires has been severely depleted or has died, leaving only tubular roots and shoots as a food and water source. Water conservation becomes a problem, and a urine hypertonic to its body fluid must be produced by $C.$ ludovicianus as one means of maintaining an internal osmotic equilibrium. Additionally, with ambient temperatures dropping below freezing and snow cover impeding daily activity, the black-tailed prairie dog is presented with a severe seasonal stress. Most sciurid hibernators avoid the situation by burrowing and remaining in a torpid state for 10-14 days at a time, arousing only to urinate and then re-entering torpor for the duration of the stress (Moy et. al., 1972). As the literature indicates, black-tailed prairie dogs remain relatively active throughout the winter and are thereby subject to the problems imposed upon a terrestrial homeotherm in the cold, without adequate food or water.

If this animal does undergo intermittent, short periods of torpor or "hibernation" during severe winter weather, then there would be a favorable energy saving. The energy cost of arousal is by far the major cost of the torpor cycle, so the longer the animal remains in a torpid condition the greater the saving. Pengelley and Fisher (1961) and Beers and Richards (1956)

studied changes in body weights of hibernators throughout the hibernating

season and determined that the loss of body weight was dependent on the

number of arousals and the length of the awake periods. In some animals,

the periodic arousals from torpor consume from 55 to 90% of the total heat

production and metabolic weight loss (Tucker, 1965). Penngelley and Fisher

(1961) suggested that this metabolic weight loss is due primarily to the

loss of water formed by the oxidation of the stored fat. Oxidation of 1.0

gram of fat yields approximately 1.08 grams of water. (Pengelley and Fisher,

1961) the retention of this water by a hibernating animal would cause a

lethal dilution of the body fluids. Metabolism during torpor produces very

little water from fat oxidation and most of this will be lost through

evaporation from the respiratory surfaces, evaporation from body surface,

and loss through urine.

Conflicting data concerning urine formation by hibernating animals is

still present in the current literature involving hibernation physiology.

Moy and Pfeiffer (1972) found that no urine is produced in the Columbian

ground squirrel (Spermophilus columbianus) during deep hibernation. Moy

(1972) determined that urine formation begins during the arousal process

from hibernation. Tempel and Musacchia (1975) in their studies with

hibernating and hypothermic golden hamsters (Mesocricetus auratus) also

found decreased urine production a low body temperatures. They found that

in both hypothermia and hibernation, there occurs a decrease in systemic

blood pressure which results in a decreased filtered load presented to the

renal tubules and, in turn a depression in their ability to transport filtered

elements. They found almost no urea and electrolyte concentration gradients

in renal tissue slices of the kidneys of both hypothermic and hibernating

hamsters. Thus, at very low body temperatures, filtration and hence excretion

might be expected to stop. Conversely, Zatzman and South (1972) obtained evidence of maintained renal function of marmots during hibernation. In a continuing study by the same researchers (1975), they demonstrated that not only did urine flow occur during hibernation (although flow was found to be low), it was measurable and hypertonic to the plasma. Zatzman and South also demonstrated that the osmotic concentration of medullary slices from the kidneys of hibernating marmots was in the range of urine osmotic concentration measured, although lower than those of normothermic animals. Additionally, they found that hibernating marmots were capable of excretion of both filtered (inulin) and secreted (PAH) materials. Passmore et. al. (1975) found a significant accumulation of serum urea in the blood of hibernating Columbian ground squirrels and concludes that the kidney is not eliminating nitrogenous wastes while the animal is torpid.

As stated earlier, the present literature on physiological studies during torpor and dehydration in the black-tailed prairie dog is very limited. There have been no published reports to date on renal function, temperature regulation, or rates of body weight loss in this animal during hibernation or dehydration. Therefore, the objectives of this study were to:

1. Study some aspects of renal function of summer dehydrated, winter dehydrated, and winter torpid black-tailed prairie dogs by:

    a) Comparing the urea and solute gradients in the kidneys, urine and plasma of these dehydrated animals.

    b) Comparing the urine to plasma (U/P) osmolal ratios between dehydrated prairie dogs.

2. Provide further evidence as to whether or not the black-tailed prairie dog is capable of undergoing periods of hibernation or intermittent torpor by:

a) Determining body temperatures during exposure to dehydration in the cold during late fall and winter.

b) Determining changes in body weight during dehydration in the cold (5-8° C) and in warm (22° C) temperatures.

CHAPTER II

MATERIALS AND METHODS

Animals

The animals utilized in this study were 19 black-tailed prairie dogs (Cynomys ludovicianus), that were live trapped from a prairie dog town located near Helena, Montana on the Ft. Harrison Military Reservation. The animals were caught in Tomahawk live animal traps that were baited with either peanut butter rolled in oatmeal or plain rolled oats. The animals' weights at capture varied from 0.5-1.2Kg, depending on the age of the animal and time of year trapped. Most were trapped in August and September of 1973 and 1974, and the majority of trapped prairie dogs were "short" yearlings.

Initially the prairie dogs were fed Purina lab chow (primarily alfalfa pellets) and were provided water daily. This feeding regimen was discontinued in August, 1974 because of the extreme weight gains (40-50% of initial body weight) made by the captive animals (some animals increased their weight to 1.9 Kg from initial weights of 0.8 to 1.0 Kg). Daily portions of lettuce, carrots and two pellets of Purina lab chow without water were substituted and weights remained fairly stable with most animals weighing between 0.9-1.4 Kg.

In October-November of 1973, eight animals were placed in a hibernaculum in metal cages with bedding material and were provided food and water, but the animals remained completely aroused. In subsequent experiments, all animals were denied food and water and three experimental groups were studied. Group I consisted of five prairie dogs that were killed while torpid (in late December to late January) with body temperatures between $10-14^\circ$ C. The animals were in a hibernaculum between 19-42 days and were exposed to T_a's between

$5-8^{\circ}$ C. Group II consisted of eight prairie dogs that were killed after being in the hibernaculum for 7-35 days (between late December 1973 to mid-March 1974). Their T_b's varied between $17-35^{\circ}$ C, with the T_a also between $5-8^{\circ}$ C. Group III consisted of six animals that were killed after 2-8.5 days without food or water (between June to October 1974). The T_a was between $20-22^{\circ}$ C with T_b varying from $32-38^{\circ}$ C. Animals in Group III were maintained in metal cages without cotton bedding material.

Experimental Procedure

The following procedures were carried out on all three groups of animals. At the termination of each experiment, an animal was removed from its cage, and its rectal T_b temperature was determined by use of a WESCO quick-registering thermometer. Body weight was determined on a Torbal torsion balance, and the sex of the animal was determined. Weights of all animals were also recorded at the beginning of each experiment. Each animal was killed by a sharp blow on the head and its left kidney was removed and immediately frozen in acetone and dry ice. A section of abdominal muscle was also removed from each animal, and terminal bladder urine and plasma samples were taken. The sectioning of the kidney and subsequent determinations of urea, sodium, and potassium concentrations in renal tissue slices, urine, and plasma followed the methodology of Moy (1972), except that the prairie dog kidney was sectioned into 5 zones instead of 6 (two cortical zones (C1 and C2), an outer medullary zone (OZ), and two inner medullary zones (IZ1 and IZ2), with IZ2 representing the tip of the papilla). A Beckman Spinco colorimeter (Model 151) was used for urea determinations. A Beckman flame spectrophotometer (Model DU) was used in determining sodium and potassium concentrations.

Standards and Controls

Four nitrogen standards were used to calibrate the colorimeter for urea

determinations. In addition, urine and serum samples, with known urea concentrations, were obtained from Hyland Laboratories and were run concurrent with each urea analysis. Five sodium and potassium standards were used to calibrate the flame spectophotometer prior to analysis. Additionally, Hyland urine and serum samples, with known sodium and potassium concentrations, were also run concurrent with each analysis. Sodium chloride standards ranging from 100-1800 mOsm/kg were tested on the Fiske Osmometer periodically with the unknown samples. Calibration standards obtained from the Advanced Instruments, Inc. were also used.

Temperature Measurement

Nine of the animals were monitored with indwelling, temperature-sensitive radio transmitters obtained from the Mini-Mitter Company (Model V). The transmitters were implanted intra-peritoneally at least one to two days prior to the beginning of an experiment. Temperature recordings were obtained hourly by using a modified AM radio receiver whose direct current (DC) output was fed into a high-gain amplifier on a Gilson polygraph (Model GME).

Experimental Groups

The three experimental groups were treated as follows:

A. Group I- Winter Torpid, Dehydrated

All animals in this group had implanted radio transmitters for continuous body temperature measurement. The animals were removed from the hibernaculum only if their T_b was below 15° C and only if they maintained this low T_b for at least 24 hours.

B. Group II- Winter Dehydrated, Active

Two of the animals in this group (#6 and #7) had implanted radio transmitters. The animals in this group had terminal T_b's varying from 17.6°-35.2° C.

C. Group III- Summer Dehydrated, Active

Two of the prairie dogs in this group had implanted radio transmitters (#15 and #17). The animals were denied food and water for varying lengths of time, urine samples were obtained by placing their cages over large polyethylene funnels. The funnels were screened to prevent fecal contamination of the urine that was channelled into a beaker containing paraffin oil and a few thymol crystals. The state of dehydration was indicated by osmolalities of urine samples collected during the time the animal was dehydrated. If the prairie dog appeared to lose its concentrating capacity (as evidenced by a dilute urine), the experiment was quickly terminated and the animal was treated as above.

Statistical Analysis

Intragroup comparisons of plasma and urine solute concentrations, and corticomedullary gradients were made using a nonparametric test (Mann and Whitney, 1947). The Mann-Whitney U-test was also used for comparing mean solute concentrations of plasma, urine and kidneys between groups of prairie dogs studied.

RESULTS

Urea Concentrations

Renal Tissue Slices

The kidneys of all summer dehydrated prairie dogs (Group III) had pronounced urea gradients extending from the cortex to the papilla (Table 1). Comparisons of urea concentrations between cortex and medulla and outer medulla and papilla showed a significant difference ($P < .05$). The kidneys of winter dehydrated prairie dogs (Group II) were comparable in those of Group III in terms of a urea gradient. The urea gradients were less in those animals killed at low body temperatures than in those killed at high body temperatures. The kidneys of torpid prairie dogs (Group I) had little or no urea gradient extending from the cortex to the papilla (Table 1). There was no significant difference ($P > .05$) in urea concentrations between the cortex and medulla or between outer medulla and papilla. Thos animals killed at a higher T_b did show a slight urea concentration gradient when compared to animals killed at a lower T_b. Table 2 and Fig. 1 represent the mean renal tissue fluid to plasma urea concentration ratios (TF/P). The TF/P of the cortex (Cl) and the papilla (IZ2) in Group III animals was 3.0 and 43.0 respectively. Mean TF/P ratios of the cortex of the papilla of Group II animals were 4.2 and 57.3. In Group I animals, these ratios were 2.6 in the outer cortex and 4.6 in the papilla. Mean urea muscle to plasma (M/P) ratios were 2.9 for Group III, 3.1 for Group II, and 2.3 for Group I animals.

Urine

The mean urea concentrations in terminal bladder urine of Group III animals (Table 1) was significantly higher (P .05) than either Group II or

12

Group I. Terminal bladder urine to plasma urea ratios (U/P) were also

higher in Group III animals (Table 7 and Fig. 4). Not all Group III

animals had bladder urine when they were killed, and therefore the last

urine collected was used to calculate urine urea concentration and U/P

ratios. Group II animals had both higher urine urea concentrations and

higher U/P ratios than Group I animals.

Plasma

The plasma urea levels between all three groups differed significantly

(P <.002), with plasma urea being most concentrated in Group III animals

(Table 1). The mean plasma urea concentrations were 9.6 mM/l for Group III,

7.5 mM/l for Group II, and 6.4 mM/l in Group I.

Sodium Concentrations

Renal Tissue Slices

The kidneys of all Group III prairie dogs had pronounced sodium gradients

extending from the cortex to the tip of the papilla (Table 3). Comparisons

of sodium concentrations between cortex and medulla and outer medulla and

papilla showed significant differences (P <.05). Group II animals showed

a more pronounced sodium gradient in their kidneys than Group III. All

Group I animals showed a slight increase in sodium concentration extending

from the cortex to the tip of the papilla. These differences between sodium

concentrations of cortex and medulla and between sodium concentrations of

outer medulla and papilla were slight but significant (p <.05).

The mean renal tissue fluid to muscle (TF/M) concentration ratios for

sodium shown in Table 4 and Fig. 2 demonstrate pronounced medullary gradients

in all groups except Group I. The mean TF/M ratios for the cortex and

papilla in Group III animals were 1.6 and 7.2 respectively, 1.5 and 8.9 for

Group II, and 1.4 and 1.8 in Group I. Mean plasma to muscle (P/M) sodium concentration ratios were 4.9 for Group III, 3.7 for Group II and 3.1 for Group I.

Urine

The concentration of sodium in the urine varied considerably between prairie dogs within all three groups. The mean sodium concentrations in terminal bladder urine of Group III animals was 66 mEq/1, 50 mEq/1 for Group II, and 35 mEq/1 in Group I animals (Table 3).

Plasma

The sodium concentrations in plasma were highest in Group III animals, with significant differences (P < .002) existing between all three groups of animals. Mean sodium plasma concentrations were 156 mEq/1 in Group III animals, 139 mEq/1 in Group II animals, and 143 mEq/1 in Group I prairie dogs (Table 3).

Potassium Concentrations

Renal Tissue Slices

No potassium concentration gradient extending from the cortex to the papilla existed in kidneys of prairie dogs of any group (Table 5). Mean potassium concentrations in kidney tissue slices were lower in Group III animals than those in Group II or I animals, but were not significantly different (P > .05).

Mean potassium renal TF/P ratios were calculated for all three groups of animals (Table 6 and Fig. 3). Again, the mean renal TF/P ratios of potassium were lower in Group III animals than in the other two groups. Terminal U/P potassium ratios were highest in Group III prairie dogs while potassium muscle to plasma (M/P) ratios were highest in Group I prairie dogs.

Urine

The urine of Group III animals possessed the highest concentration of potassium with a mean value of 165 mEq/l. The mean potassium concentrations in the urine of Group II animals was 55 mEq/l, with Group I having a mean concentration of 62 mEq/l, but there was considerable variation in both groups.

Plasma

There was no significant difference (P > .05) in plasma potassium concentrations between Groups. The mean plasma potassium concentrations for the three groups were 8.0 mEq/l for Group III, 8.7 mEq/l for Group II, and 7.5 mEq/l for Group I prairie dogs.

Osmolality

Group III animals had the most concentrated urine and plasma (Table 7), with mean values of 1614 mOsm/kg and 340 mOsm/kg respectively. Group II animals had a mean urine osmolality of 972 mOsm/kg and a mean plasma osmolality of 318 mOsm/kg. Group I animals had the most dilute urine and plasma, with mean values of 726 mOsm/kg and 313 mOsm/kg respectively. Osmolal urine to plasma ratios (U/P) were determined for all three groups of animals (Table 7). Group III animals showed the highest ratios and Group I the lowest ratios. Figure 4 shows the relationship between U/P osmolal ratios and dehydration time for all three groups of animals.

Body Weight Loss During Dehydration

Both per cent of initial weight lost and amount of weight lost per kilogram of initial body weight/day, during the experiments, were calculated for all groups of prairie dogs (Table 8). Group I animals had the highest mean % body weight loss (31%), but lost less weight during their time in

dehydration (10.2 g/kg/day) when compared to Group II and III animals.
Group III animals lost the most weight during their short time in
dehydration (40 g/kg/day), but had the lowest mean % body weight loss
(11%). Group II prairie dogs lost 28% of their body weight while dehydrated,
with an average daily weight loss of 14.0 g/kg/day. Figure 5 shows the
relationship between weight loss during the time dehydrated, in all three
groups of animals.

<u>Body Temperature Measurements</u>

Because all Group I animals had implanted radio transmitters, changes
in T_b over different periods of time were determined. All of the animals
in this group showed the same basic cycle of T_b changes (See Fig. 6). A
typical animal in this group would remain completely active in the hibernaculum
from 7-10 days, maintaining its T_b between 32-38° C. The next 10 days would
be characterized by short, intermittent drops in T_b (i.e. 17° C, 14° C, 12° C),
and the animal would remain at these T_b's for a period of a few hours to a
day. Eventually, after the prairie dog had been in the hibernaculum for
approximately 15 days, these intermittent drops in T_b would become less
frequent, with T_b usually becoming lower each time and duration of torpor
increasing from a few hours to 2-3 days. The T_b cycles of all animals in
this group was characterized by the same phenomenon: when they started to
lower their body temperature, they did so in a very rapid fashion (6-8 hours).
Rarely, did any of these animals remain at an intermediate T_b (ie. 20° C)
before arriving at its minimum T_b (13° C). The rate of arousal was even
more rapid than that of decline into torpor (4-5 hours). One prairie dog
in this group raised its T_b from 12.8^O C to 35° C in three hours, while at
a T_a of 6.0^O C. As Figure 6 indicates, once an animal had been in the

hibernaculum for approximately 20 days, its T_b when aroused was usually between 31-34° C rather than the normal homeothermic range of 35-38° C. The prairie dogs in this group had T_b's between 8.2-38° C, with most of torpid animals maintaining a T_b below 20° C approximately 30% of the time. Only two prairie dogs in Group II had implanted transmitters (See Fig. 7) and both of these animals remained completely active (T_b between 33-38° C) throughout the experiment (30 days from late-January late February). The remaining six animals in this group that were monitored periodically had rectal temperatures varying from 17.6-35.2° C. The two instrumented animals in Group III had radio transmitters that changed frequency midway through the experiment. Therefore exact temperature measurements were not recorded, but the data suggest that there was little deviation from a normal T_b range (36-38° C) while the prairie dogs were dehydrated. Terminal body temperatures in this group varied from 32.8° C to 38.0° C, with a mean value of 35.6° C (appendix).

Table 1

MEAN UREA CONCENTRATIONS IN RENAL TISSUE SLICES,

PLASMA AND URINE

mM/l

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
Cl	17±7.1	28±16.5	29±10.4
C2	19±10.0	66±38.0	69±27.0
OZ	23±10.6	213±84.8	284±63.0
IZ1	25±10.0	312±152.0	413±104.0
IZ2	30±19.0	435±209.0	503±100.0
Muscle	14±5.3	22±8.0	27±22.0
Plasma	6.4±0.5	7.5±1.8	9.6±2.1
Terminal Bladder Urine	385±104.0	553±220.0	856±150.0

Table 2

MEAN UREA TISSUE FLUID TO PLASMA (TF/P), URINE TO PLASMA (U/P),

AND MUSCLE TO PLASMA (M/P) RATIOS

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
C1	2.6±1.1	4.2±3.6	3.0±1.3
C2	3.0±1.5	9.1±5.6	7.2±2.8
OZ	3.5±1.6	28.9±11.6	29.9±7.9
IZ1	3.8±1.6	38.1±21.6	43.5±12.8
IZ2	4.6±3.1	57.3±27.4	52.8±11.5
Terminal U/P	60.8±15.3	70.1±21.0	90.7±23.3
M/P	2.3±0.9	3.1±2.0	2.9±1.2

19

UREA GRADIENTS

-normothermic-III
-winter active-II
-winter torpid-I

C-1
C-2
OZ
IZ-1
IZ-2

5 10 15 20 25 30 35 40 45 50 55

TF/P urea
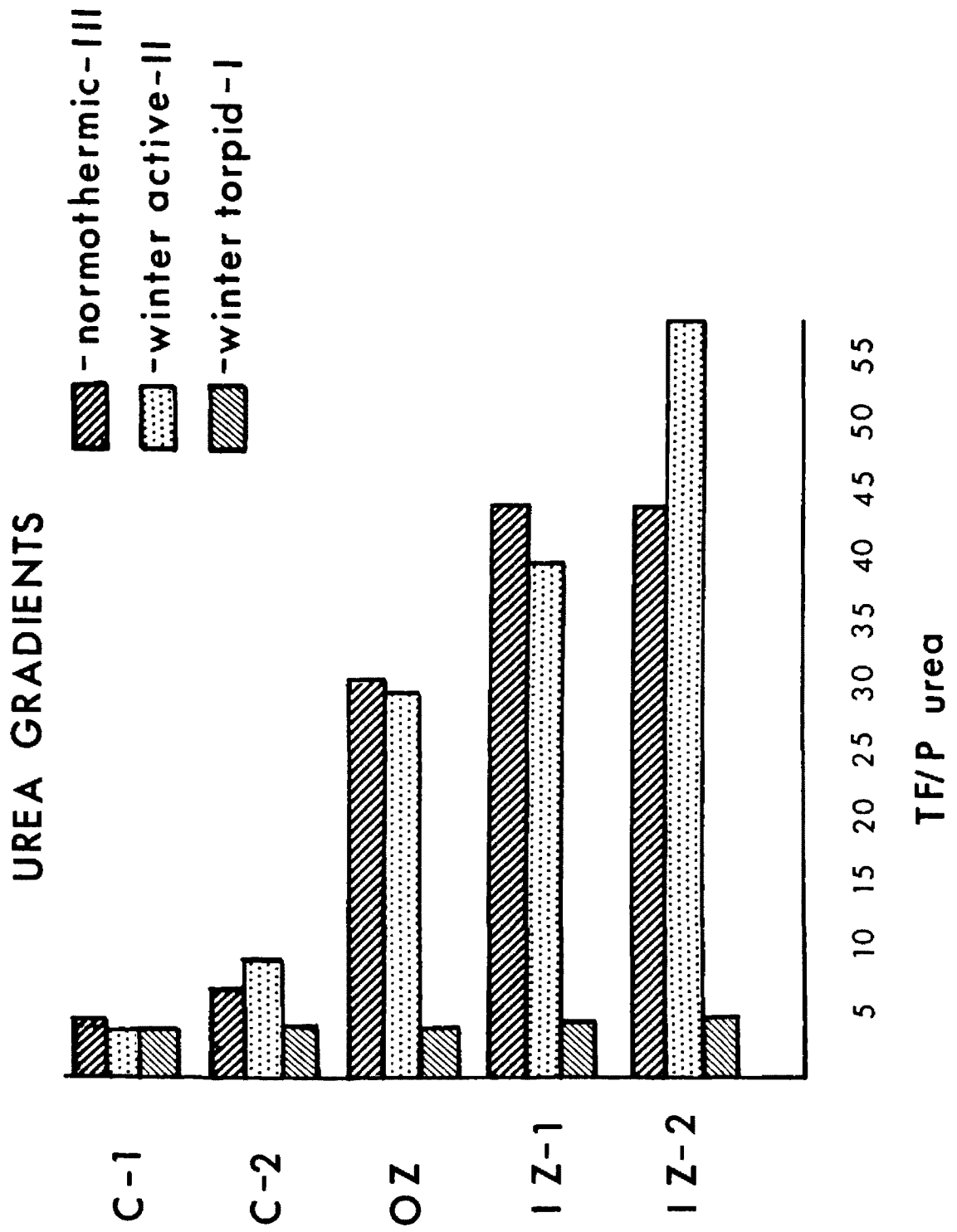
Table 3

MEAN SODIUM CONCENTRATIONS IN RENAL TISSUE SLICES,

PLASMA AND URINE

mEq/l

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
C1	67±10.8	63±22.2	55±15.5
C2	66±9.8	117±61.2	82±14.9
OZ	73±7.6	220±78.7	157±44.5
IZ1	77±8.0	273±85.4	201±48.8
IZ2	86±8.2	338±73.6	242±56.0
Muscle	47±15.3	40±13.7	34±11.3
Plasma	143±3.4	139±9.3	156±2.8
Terminal Bladder Urine	35±29.7	50±50.8	66±47.4

Table 4

MEAN SODIUM TISSUE FLUID TO MUSCLE (TF/M)
AND PLASMA TO MUSCLE (P/M) RATIOS

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
C1	1.4±0.3	1.5±0.3	1.6±0.3
C2	1.4±0.4	2.9±1.0	2.5±0.8
O2	1.6±0.4	5.6±1.3	4.7±1.1
IZ1	1.6±0.5	7.0±1.8	6.1±1.6
IZ2	1.8±0.4	8.9±4.6	7.2±1.2
P/M	3.1±0.7	3.7±1.2	4.9±1.5

Fig. 2. Histogram of mean renal tissue fluid to muscle sodium concentration ratios (TF/M). Group III = normothermic (n = 6), Group II = winter active (n = 8), Group I = winter torpid (n = 5).

SODIUM GRADIENTS
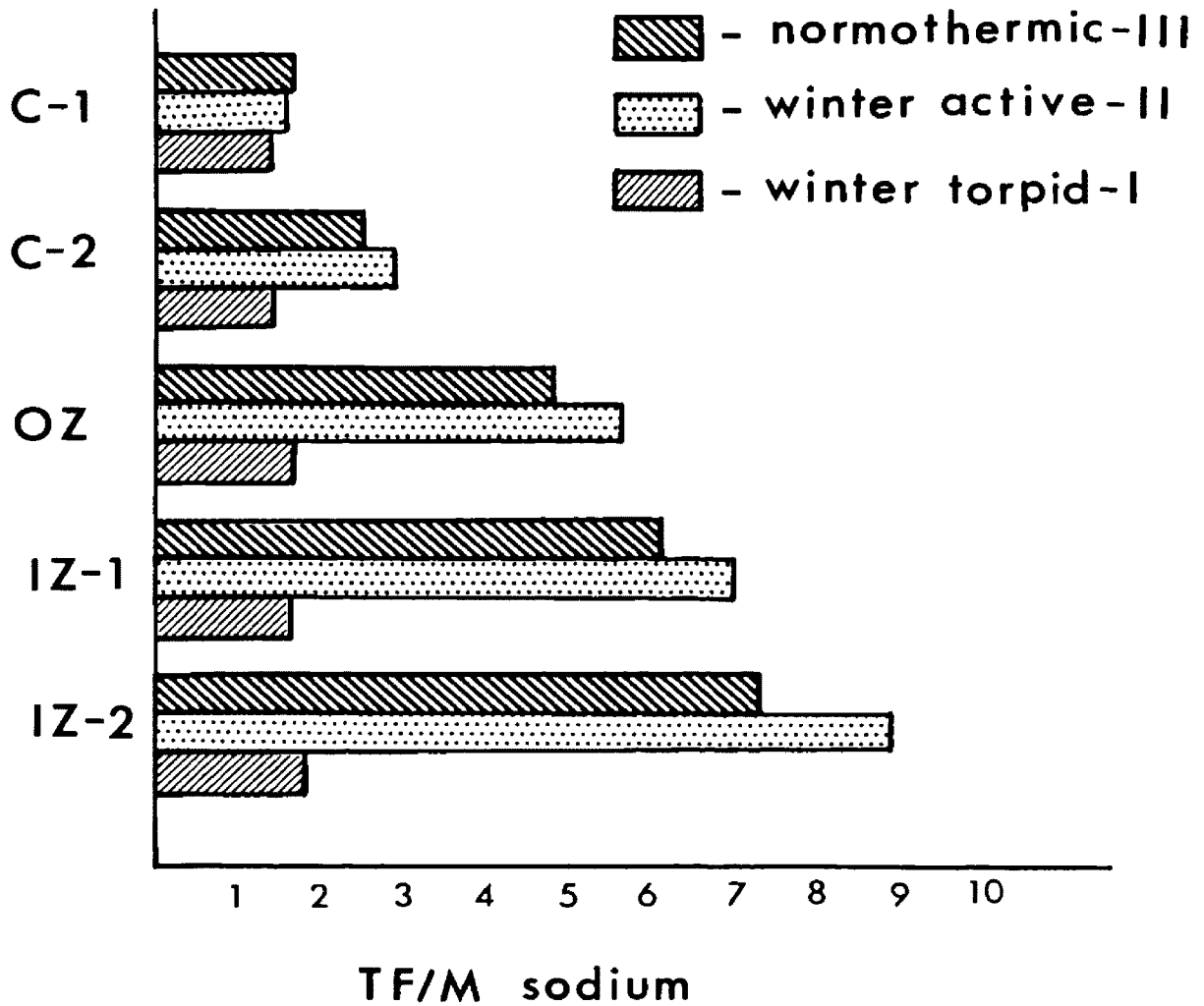
Table 5

MEAN POTASSIUM CONCENTRATIONS IN RENAL TISSUE SLICES,

PLASMA, AND URINE IN mEq/l

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
C1	79±7.3	77±18.0	66±8.6
C2	74±8.4	77±19.0	66±9.9
OZ	75±8.0	76±18.9	65±4.6
IZ1	76±7.9	79±19.5	65±7.0
IZ2	75±6.9	78±5.7	++
Muscle	123±13.3	108±13.3	111±9.4
Plasma	7.5±1.3	8.7±2.9	8.0±1.1
Terminal Bladder Urine	61±26.5	55±27.9	164±21.7

Table 6

MEAN POTASSIUM TISSUE FLUID TO PLASMA (TF/P), URINE TO PLASMA (U/P) AND MUSCLE TO PLASMA (M/P) RATIOS

Sample	Group I Torpid Prairie Dogs	Group II Winter Aroused Prairie Dogs	Group III Normothermic Prairie Dogs
C1	11.4±1.6	10.2±5.3	8.3±1.8
C2	10.2±1.8	10.2±5.4	8.3±1.9
OZ	10.3±2.0	8.9±3.9	8.2±1.5
IZ1	10.3±2.0	10.3±5.2	8.2±1.4
IZ2	10.7±1.3	8.2±0.8	++
Terminal U/P	8.9±5.2	8.0±4.0	21.2±1.9
M/P	15.5±3.1	13.3±6.3	13.9±2.1

++ = No Sample Available

Fig. 3. Histogram of mean renal tissue fluid to plasma potassium concentration ratios (TF/P). Group III = normothermic (n = 6), Group II = winter active (n = 8), Group I = winter torpid (n = 5).

POTASSIUM GRADIENTS

- normothermic- III
- winter active- II
- winter torpid- I

TF/P potassium
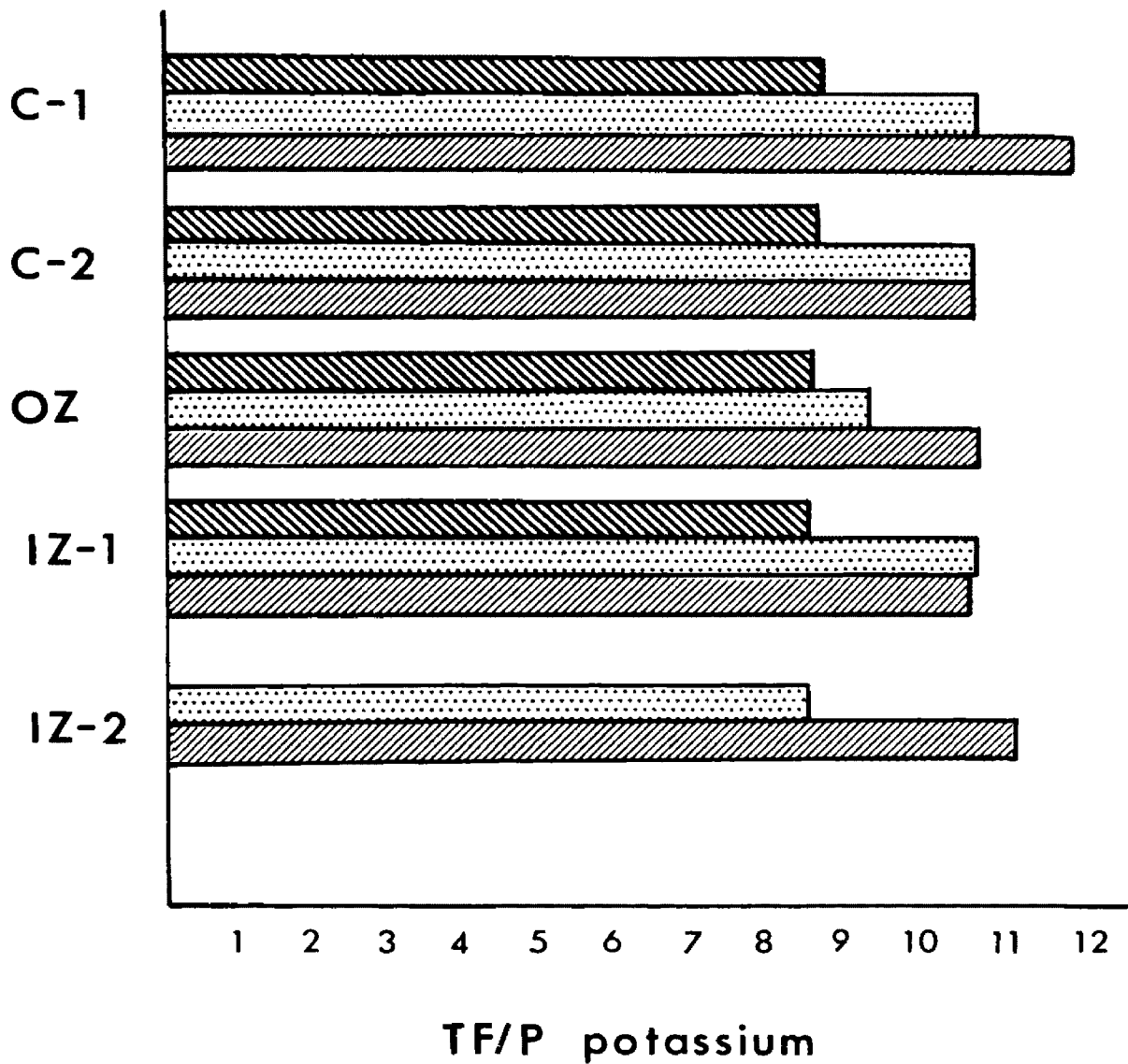
Table 7

TERMINAL URINE AND PLASMA OSMOLALITIES (mOsm/kg)

AND OSMOLAL U/P RATIOS

Animal No.	Plasma	Urine	U/P Ratio	Days Dehydrated
Group III				
# 13	340	1900	5.6	2
# 14	336	1825	5.4	2
# 12	349	1700	4.8	2
# 16	340	1160	3.4	2
# 15	330	1200	3.6	3
# 17	345	1900	5.5	8.5
Mean	340	1614	4.7	3.25
Group II				
# 2	300	630	2.1	17
# 5	290	340	1.2	11
# 1	298	762	2.5	26
# 8	327	656	2.0	7
# 4	347	++	++	35
# 10	300	1550	5.2	29
# 7	345	1800	5.2	32.5
# 6	337	1070	3.2	32
Mean	318	972	3.1	23.7
Group III				
# 18	300	620	2.0	30.5
# 19	315	980	3.1	34
# 20	320	1000	3.1	42
# 21	320	605	1.9	19
# 22	310	428	1.4	30
Mean	313	726	1.7	31.1

++ = No Sample Available

Fig. 4. Relationship between osmolal U/P ratios and days without food and water for all three groups of animals.

DAYS DEHYDRATED

U/P osm

▲ -normothermic - III
■ -winter active - II
● -winter torpid - I
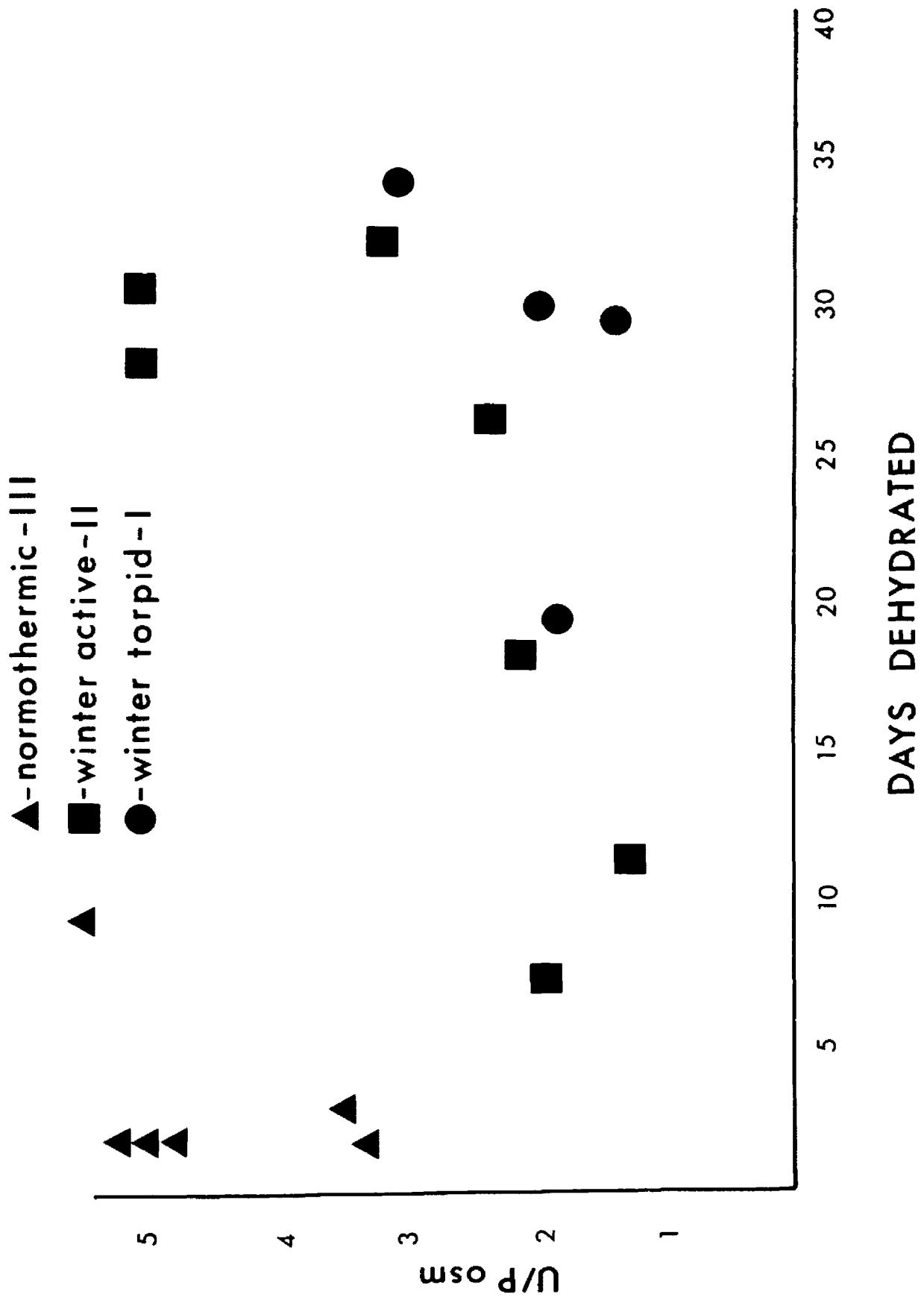
Table 8

PER CENT BODY WEIGHT LOSS AND AVERAGE WEIGHT LOST
PER Kg INITIAL WEIGHT PER DAY

Animal No.	Initial Body Weight (g)	% B.W. Loss	g lost/kg/day
Group III			
# 13	1076	6.9	34.4
# 14	1320	7.0	34.8
# 12	1502	5.9	30.0
# 16	1183	15.1	75.6
# 15	820	15.0	50.0
# 17	1069	14.0	16.5
Mean	1161	10.6	40.2
Group II			
# 2	941	27.8	16.3
# 5	930	16.5	15.0
# 1	927	36.8	14.1
# 8	975	11.9	17.0
# 4	1024	32.4	9.3
# 10	1004	34.8	12.0
# 7	1353	37.1	11.4
# 6	1325	47.2	14.7
Mean	1060	30.5	13.7
Group I			
# 18	936	29.7	9.7
# 19	1119	23.6	9.0
# 20	1122	47.0	11.1
# 21	956	17.3	9.0
# 22	1005	36.0	12.0
Mean	1027	30.7	10.2

Fig. 5. The relationship between weight loss (g/kg B.W./day) and the number of days each animal was dehydrated in black-tailed prairie dogs.

g lost/kg/day

Days Dehydrated

▲−normothermic−III
■−winter active−II
●−winter torpid−I
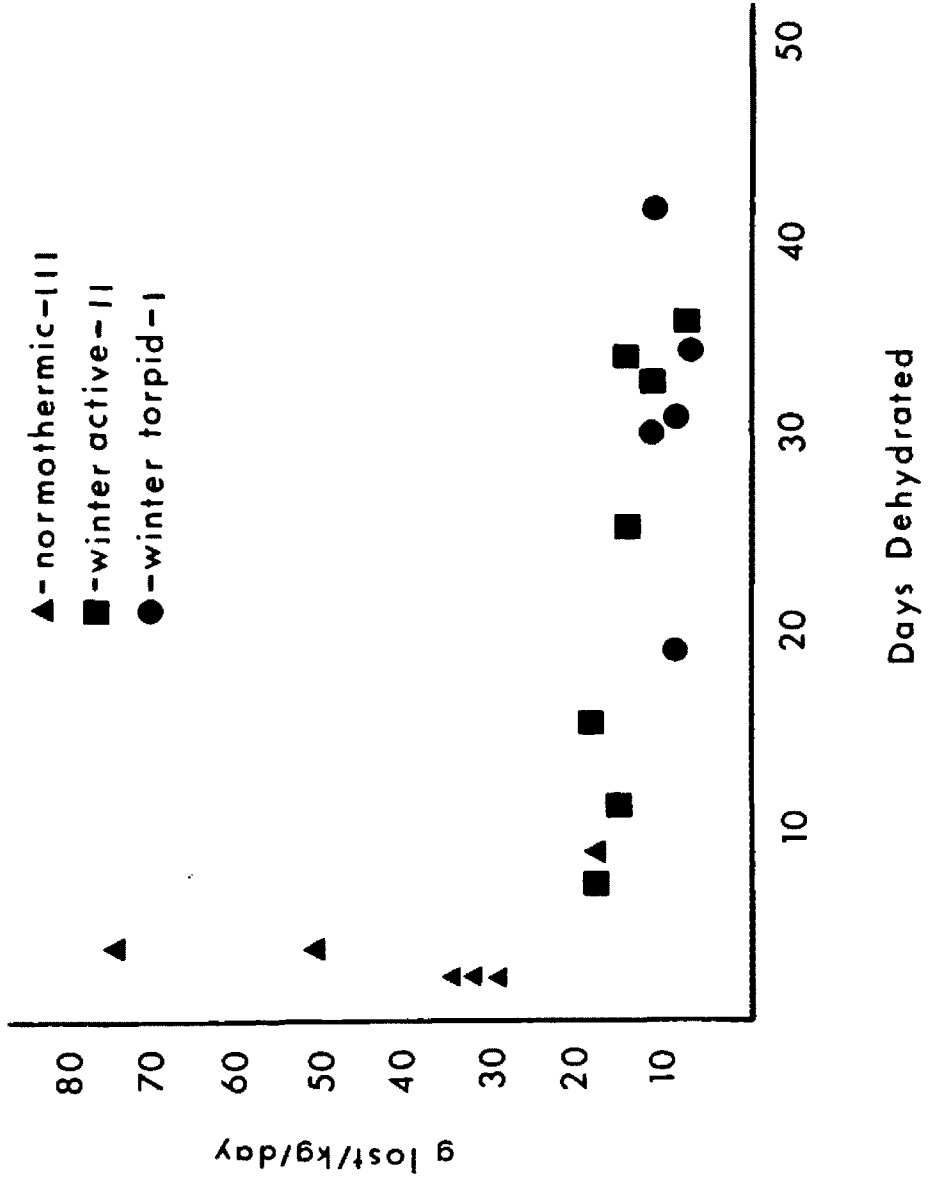
Fig. 6. A typical temperature cycle observed in a prairie dog between late October-mid January. Each dot represents a separate body temperature recording obtained from an animal while at an ambient temperature of 7° C.

winter torpid prairie dog
Ta=7°C

Body Temperature °C

Days in Hibernaculum
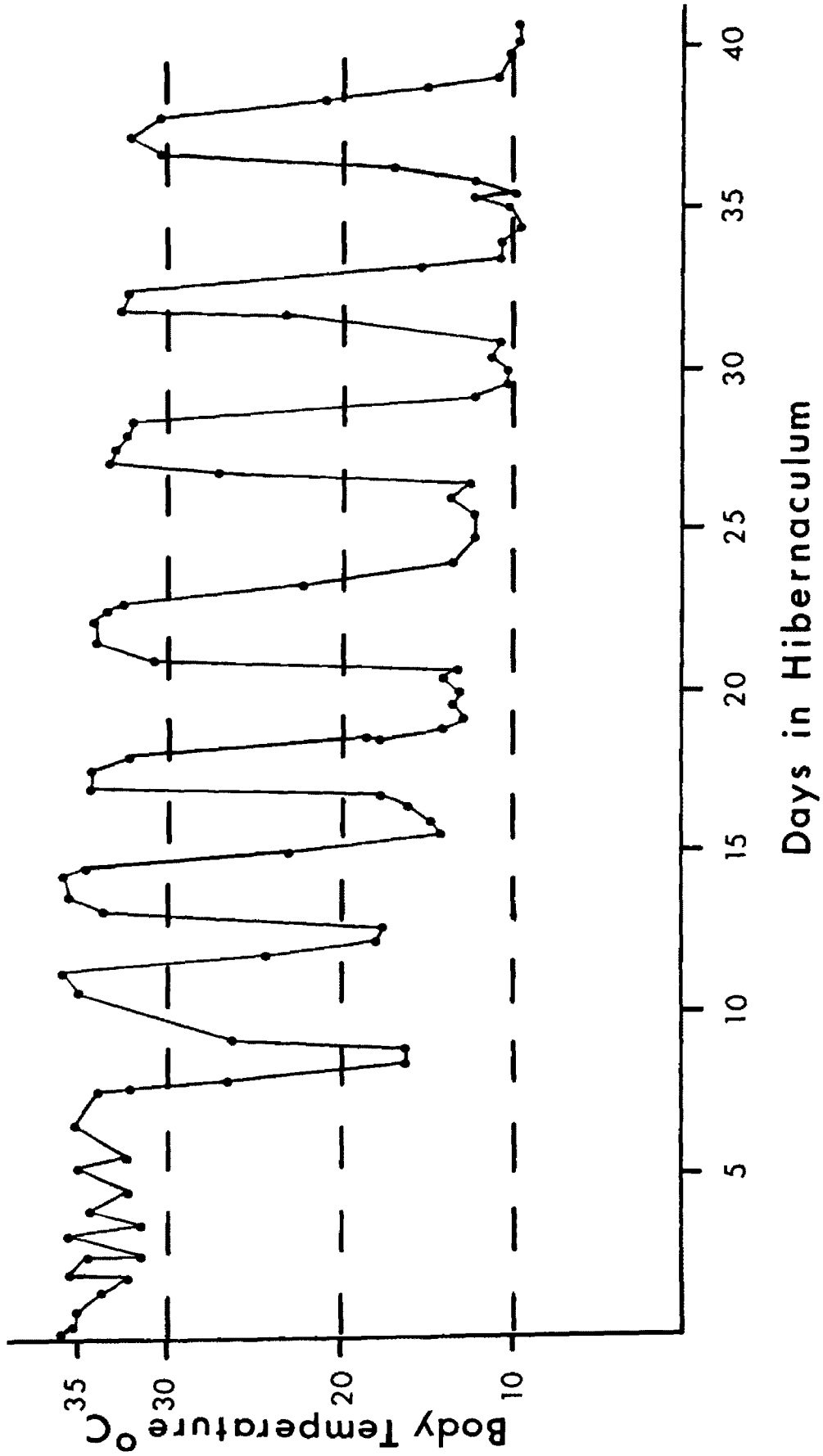
Fig. 7. A typical temperature cycle observed in a prairie dog between late January and mid March. Each dot represents a separate body temperature recording obtained from an animal while at an ambient temperature of 7° C.

winter active prairie dog

Ta = 7°C

Body Temperature °C

Days in Hibernaculum
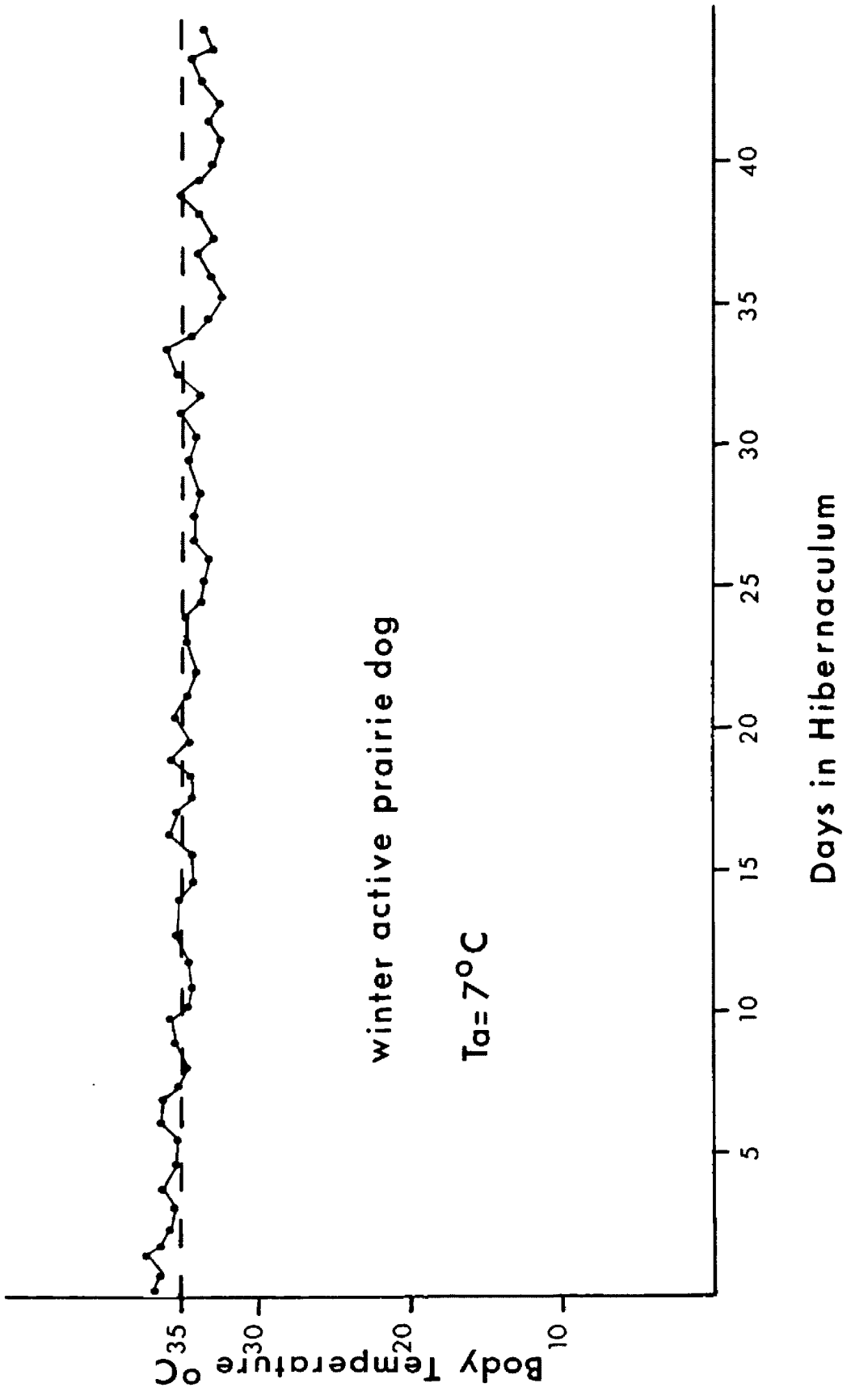
CHAPTER IV

DISCUSSION

The results of this study show that certain aspects of renal function in the black-tailed prairie dog (Cynomys ludovicianus) during torpor and arousal are very similar to those described by Moy (1971) in Columbian ground squirrels and by Tempel and Musacchia (1975) in golden hamsters. During torpor, there is no renal corticomedullary urea gradient and no significant sodium gradient. As in all other species studied, there was no potassium gradient in the kidneys of any prairie dogs. The absence of a corticomedullary solute gradient during torpor suggests a lack of glomerular filtration, because filtration is needed to produce such a gradient (Jamison et. al. 1967).

Because bladder urine was hypertonic to the plasma in torpid prairie dogs, most of it could not have been produced during torpor because of the lack of a medullary gradient. It is possible, of course, that some isosmotic urine was filtered although this is unlikely in view of the information cited above (Jamison ibid).

Urea concentrations were considerably higher in the plasma of both active summer and winter dehydrated prairie dogs than in winter torpid animals, which suggests that protein catabolism with subsequent nitrogen accumulation in the tissues is reduced in torpid prairie dogs. These data are similar to those of Galster and Morrison (1975), who found lower concentrations of urea nitrogen in the plasma of arctic ground squirrels (Citellus undulatus) during hibernation than in those during summer fasting and during the late arousal period. The low plasma urea concentrations found in torpid animals and the ability of these animals

33

to maintain water balance (plasma osmotic concentrations rose very little) suggest that this species of prairie dog reduces protein catabolism during torpor and uses some other energy substrate, whose oxidation produces adequate water to maintain fluid balance.

The fact that sodium and osmotic concentrations were higher in the plasma of both summer and winter dehydrated prairie dogs when compared to winter torpid animals, is further evidence of a difference in energy substrates between torpid animals and the other two groups.

If torpid prairie dogs metabolized only fat during arousal, then the water liberated during oxidation of the fat would dilute the body fluids. Aroused (normothermic) prairie dogs may be using some other energy source (ie. lean body mass), thereby increasing the osmotic concentration of the body fluids. The urinary sodium concentrations were quite variable within the three groups and were significantly reduced in both winter dehydrated and torpid animals. The low urine sodium excretion in animals undergoing periods of torpor may have been the result of increased aldosterone levels inducing tubular reabsorption of sodium in response to decreasing plasma sodium during arousal and entry into torpor (Morris and Davis, 1974). Yaakobi and Shkolnik (1974) found high urine sodium concentrations in dehydrated, non-torpid hedgehogs similar to the high concentrations found in summer dehydrated prairie dogs. Bakko (1975) found high sodium plasma concentration in dehydrated red and gray squirrels when compared to hydrated squirrels in the lab and the same squirrels in the field.

Because both winter dehydrated and winter torpid prairie dogs had lower urine potassium concentrations but similar plasma potassium concentrations than those of summer dehydrated animals, the kidneys of both of

these winter dehydrated animals apparently were conserving potassium in response to the lack of potassium intake. The Group III normothermic animals apparently were not conserving potassium during the time they were dehydrated.

The ratios presented in the tables reveal considerable diversity of physiologic states among the three groups of dehydrated animals. The renal tissue fluid to plasma and muscle to plasma ratios for urea were considerably higher in both summer and winter dehydrated animals than in winter torpid animals, which is further evidence that these animals are producing less nitrogenous metabolic products than the other groups.

Terminal osmolal U/P ratios were higher in summer and winter dehydrated animals than in torpid animals, which gives some indication of the osmotic state of these animals. A high U/P ratio suggests that the animal is in a stressed condition (dehydrated) and is actively trying to conserve water. A low U/P ratio suggests than an animal is adequately hydrated and that water conservation is not an immediate problem.

The sodium P/M ratios give a good indication of dehydration among the three groups, with torpid animals having the lowest ratio. The decrease of sodium concentrations in the plasma coupled with an increase of sodium concentration in the muscle without sodium intake, may indicate that water is moving from intracellular to extracellular fluid compartments in response to the dehydration stress.

Group III summer dehydrated prairie dogs had the lowest potassium concentrations in kidney tissue slices, lowest potassium TF/P ratios, highest potassium concentrations in the urine, and the highest potassium U/P ratios, which strongly suggests that more potassium is lost during the initial active dehydration phase than during torpor. The potassium

M/P ratios as well as the sodium M/P were highest in torpid animals, suggesting that a possible movement of water from intracellular to extra-cellular fluid compartments is taking place. This would increase the potassium concentration muscle cells, much the same as with sodium.

Although the body weight loss on a per day basis was highest in summer dehydrated animals, this figure is somewhat misleading. The animals in this group urinated and defecated quite readily during the short time that they were dehydrated. Limited studies by other researchers (Personal Communication, Ron Wheeler), of weight loss during dehydration at room temperature and in the cold ($T_a=6^0$ C) during the summer, have shown that if the dehydration period is extended to the same duration as that of animals dehydrated in the winter, the average weight loss approximates that found in the two other groups. Animals dehydrated in the winter that remained active throughout the dehydration period had substantially higher per day weight losses than animals in either groups. With some exceptions, the primary energy source for an active dehydrated animal, whether in the cold or in a T_a of 20° C, is fat lipolysis (Galster and Morrison,1970). The respiratory quotient of hibernating animals approaches 0.7, suggesting that lipid rather than carbohydrate is the principal metabolite being utilized (Tashima et. al., 1970). The evidence from this study suggests that lipid is the chief energy source for prairie dogs which are not fed or watered.

Galster and Morrison (1975) found normal levels of plasma lactate, FFA, glycerol and triglycerides of active ground squirrels force-fasted in both summer and winter but plasma urea levels increased to 2-3 times higher than normal concentrations found in man. This would suggest that protein catabolsim with subsequent increased urea production, is taking

place using lean body mass as the energy source. In hibernating animals, they found a decrease in all of these levels late in the torpor period, suggesting that glucose reserves are restored by lipolysis during arousal, with minimal protein catabolism. Nelson et. al. (1975) found that torpid bears in the winter inhibit the net production of urea and maintain constant lean body mass during the winter sleep by metabolizing only fat as a source of energy. They found that the bear could not duplicate this feat during the summer when starved outside under ambient temperature or when housed in a hibernaculum. Owen (1969) demonstrated that there is a reduction in the total amount of glucose produced during prolonged starvation. He found that about one-half of the formed glucose during starvation is derived from recycled lactate and pyruvate. The remaining glucose was derived from glycerol released from triglycerides and amino acids mobilized from proteins. Owen states that "a reduction in protein catabolism during prolonged starvation is mandatory for survival".

Further studies by other researchers (Wheeler, ibid) with two prairie dogs placed in a hibernaculum in the summer for more than 15 days, showed weight losses slightly greater than for two animals that were dehydrated at room temperature for the same amount of time. The weight loss incurred by those animals placed in a hibernaculum in the summer most closely approximated the weight loss of the Group II winter dehydrated animals. Group I torpid animals had the least weight loss on a per day basis while dehydrated, and presumably this is because of a very great decrease in urine production and the intermittent periods of torpor that these animals underwent. The large number of arousals appear to be very expensive energetically. A possible explanation for the large number of arousals, would be depletion of glucose reserves during torpor and the

need to arouse to carry out gluconeogenesis. This situation has been demonstrated in several hibernators by Galster and Morrison (1975). Galster and Morrison (1975) report that the glucose reserves of some hibernators (Citellus undulatus, C. tridecemlineatus, Eliomys quercinus, Erinaceus europoeus) dwindle during hibernation. The glucose reserves are apparently restored during brief homeothermal periods that divide the season into a series of short, two week hibernation cycles.

The body temperature measurements showed that these animals do not undergo any drastic changes in T_b while dehydrated at room temperature. The longest dehydration period for a Group III animal was 8.5 days and the T_b in this animal fluctuated between 32-38° C.

All Group I animals showed a similar pattern of body temperature fluctuations while in the hibernaculum from late October to late January. This pattern is unlike that found in many Sciurid hibernators that "linger" at certain low T_b's for a few hours to a day before continuing a steady decline in T_b approximating the ambient temperature (Strumwasser, 1960). The body temperature measurements show unequivocally that black-tailed prairie dogs are capable of lowering their T_b close to the ambient temperature in the winter and are capable of sustained periods of torpor.

Two Group II winter dehydrated prairie dogs maintained their T_b's between 32-38° C for more than 30 days from late January to late February. This suggests that this species adheres to some cyclical seasonal patterns of torpor related to reproduction, because some torpid females killed during the same period exhibited swollen ovaries and corpora hemorhagica These animals normally breed from late January through February, and they would not be expected to continue hibernating during this period. But studies by other researchers (Ron Wheeler, ibid) have shown that the

black-tailed prairie dog is capable of lowering its T_b below 10° C while dehydrated in a hibernaculum ($T_a=6^{\circ}$ C) in the summer, after its breeding season. Thus, it may be that torpor is impossible during the active reproductive period.

This study shows that the black-tailed prairie dog is a "facultative hypotherm", except during the breeding season. Further study is needed to clarify the role that torpor and arousal play in this animal's responses to cold, dehydration, food deprivation and reproduction.

CHAPTER V

SUMMARY

While torpid in the winter, black-tailed prairie dogs do not possess a sodium or urea renal concentration gradient extending from the cortex to the papilla. Active prairie dogs in the summer and winter possess pronounced renal medullary sodium and urea concentration gradients. No potassium concentration gradient exists in the kidneys of black-tailed prairie dogs at any time.

Comparison of body fluid osmotic concentrations show that torpid prairie dogs are less dehydrated than active animals that are denied food and water in the summer and winter. Urea does not tend to accumulate in the bood of prairie dogs during torpor.

During dehydration in the winter, body weight loss is probably due primarily to fat metabolsim, sparing lean body mass in the animal. When denied food and water in the cold, the black-tailed prairie dog undergoes short periods of torpor interspersed with short arousals (except during the breeding season). During torpor, the body temperature of the prairie dog closely approximates the ambient temperature.

40

LITERATURE CITED

Anthony, A. 1955. Behavior patterns in a laboratory colony of prairie dogs, Cynomys ludovicianus. J. Mamm., 36: 69-78.

Bakko, E. G. 1975. A field water balance study of gray squirrels (Sciurus carolinensis) and red squirrels (Tamiasciurus hudsonicus). Comp. Biochem. Physiol., 51A: 759-768.

Beers, J. and A. G. Richards. 1956. Hibernation in the big brown bat. J. Mamm., 37: 31-41.

Boice, R. and J. A. Witter. 1970. Motivating prairie dogs. Psychon. Sci., 20: 287-289.

Brown, D. C., Mulhausen, R. O., Andrew, D. J. and U. S. Seal. 1971. Renal function in anesthesized dormant and active bears. Am. J. Physiol., 220: 293-298.

Folk, G. E. 1966. Introduction to environmental physiology. Lea and Febiger, Philadelphia, 308 pp.

Galster, W. A. and P. R. Morrison. 1970. Cyclic changes in carbohydrate concentrations during hibernation in the arctic ground squirrel. Am. J. Physiol., 218: 1228-1232.

Galster, W. and P. R. Morrison. 1975. Gluconeogenesis in arctic ground squirrels between periods of hibernation. Am. J. Physiol., 228: 325-330.

Hoffman, R. A. 1964. Terrestrial animals in cold: hibernators. In: Handbook of Physiology, Sec. 4, Adaptation to the Environment. D. B. Dill, sec. ed. Amer. Physiol. Soc.

Hudson, J. W. and G. A. Bartholomew. 1964. Terrestrial animals in dry heat: estivators. In: Handbook of Physiology, Sec. 4, Adaptation to the Environment. D. B. Dill, sec. ed. Amer. Physiol. Soc.

Jamison, R. L., Bennett, C. M. and R. W. Berliner. 1967. Counter-current multiplication by the thin loops of Henle. Am. J. Physiol., 212: 357-366.

King, J. A. 1955. Social behavior, social organization, and population dynamics in a black-tailed prairie dog town in the Black Hills of South Dakota. Contrib. Lab. Vert. Biol., Univ. of Michigan, 67: 1-123.

Mann, H. O. and D. R. Whitney. 1947. On a test of whether one of two random variables is stochastically larger than the other. Am. Math. Statist., 18: 50-60.

41

Morris, D. L. and R. P. Davis. 1974. Aldosterone: current concepts. Metabolism, 23: 473-494.

Morrison, P. 1960. Some interactions between weight and hibernation function. Bull. Museum Comp. Zool. Havard Coll., 124: 75-91.

Moy, R. M. 1971. Renal function in the hibernating ground squirrel (Spermophilus columbianus). Amer. J. Physiol., 220: 747-753.

Moy, R. M., Lesser, R. W. and E. W. Pfeiffer. 1972. Urine concentrating ability of arousing and normothermic ground squirrels (Spermophilus columbianus). Comp. Biochem. Physiol., 41A: 327-337.

Nelson, R. A., Jones, J. D., Wahner, H. W., McGill, D. B. and C. F. Code. 1975. Nitrogen metabolism in bears: urea metabolism in summer starvation and in winter sleep and role of urinary bladder in water and nitrogen conservation. Mayo Clin. Proc., 50: 141-147.

Owen, O. E. and P. Felig. 1969. Liver and kidney metabolism during prolonged starvation. J. Clin. Invest., 48: 574-583.

Passmore, J. C., Pfeiffer, E. W. and J. R. Templeton. 1975. Urea excretion in the hibernating columbian ground squirrel (Spermophilus columbianus). J. Exp. Zool., 192: 83-86.

Pengelley, E. T. and K. C. Fischer. 1961. Rhythmical arousal from hibernation in the golden-mantled ground squirrel (Citellus lateralis tescorum). Can. J. Zool, 39: 105-120.

Schmidt-Nielsen, B. and R. O'Dell. 1958. Effect of diet on the distribution of urea and electrolytes in kidneys of sheep. Am. J. Physiol., 197: 856-860.

Smith, R. E. 1958. Natural history of the prairie dog in Kansas. Mus. Nat. Hist. Misc. Pub., 16: 1-36.

Strumwasser, F. 1960. Some physiological principles governing hibernation in Citellus beecheyi. In: Mammalian hibernation, C. P. Lyman and A. R. Dawe, ed., Bull. Museum Comp. Zool. Harvard Coll., 124: 285-320.

Tashima, L. S., Adelstein, S. J. and C. P. Lyman. 1970. Radioglucose utilization by active, hibernating, and arousing ground squirrels. Am. J. Physiol., 218: 303-309.

Tempel, G. E. and X. J. Musacchia. 1975. Renal function in the hibernating and hypothermic hamster (Mesocricetus auratus). Am. J. Physiol., 22: 602-607.

Tileston, J.V. and R. R. Lechleitner. 1966. Some comparisons of the black-tailed and white-tailed prairie dogs in north-central Colorado. Am. Midl. Nat., 75: 292-316.

Tucker, V.A. 1965. The relation between the torpor cycle and heat exchange in the California pocket mouse (Perognathus californicus). J. Cell. Comp. Physiol., 65: 405-414.

Yaakobi, D. and A. Shkolnik. 1974. Structure and concentrating capacity in kidneys of three species of hedgehogs. Am. J. Physiol., 226: 948-952.

Zatzman, M.L. and F. E. South. 1972. Renal function in the awake and hibernating marmot (Marmota flaviventris). Amer. J. Physiol., 22: 1035-1039.

Zatzman, M.L. and F. E. South. 1975. Concentration of urine by the hibernating marmot. Amer. J. Physiol., 228: 1336-1340.

APPENDIX

1

UREA CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

Group III SUMMER DEHYDRATED ANIMALS

mM/l

Prairie Dog No./Sex	13-♂	14-♂	15-♂	16-♂	15-♀	17-♂	Mean
C1	45.7	28.1	15.4	21.4	33.5	29.0	28.8
C2	51.1	72.3	75.6	31.2	112.5	71.6	69.0
OZ	274.0	342.8	240.0	218.6	378.9	249.4	283.9
IZ1	363.1	534.6	345.9	292.9	549.0	391.2	412.8
IZ2	455.0	542.7	513.4	326.6	586.9	593.6	503.0
Muscle	45.1	26.0	15.2	21.7	29.6	26.7	27.4
Plasma	8.6	8.6	9.0	10.7	10.0	10.8	9.6
Terminal Bladder Urine	1091	943.5	768.4	671.5	772.4	890.3	856.2
Body Temperature at Sacrifice °C	35.2	35.5	34.8	37.5	32.8	38.0	35.6

2

UREA CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

Group II WINTER DEHYDRATED ANIMALS

mM/l

Prairie Dog No./Sex	5-♀	10-♀	2-♀	1-♀	4-♂	8-♀	7-♂	6-♂	Mean
C1	64.1	23.4	36.0	23.1	10.2	19.9	18.9	31.7	28.4
C2	61.6	99.8	133.8	67.6	15.4	79.4	46.6	27.6	66.5
OZ	150.8	259.3	272.5	271.6	92.6	343.5	157.9	160.3	213.6
IZ1	180.4	++	328.0	282.6	108.4	581.2	321.6	383.8	312.3
IZ2	199.0	613.5	440.5	330.3	124.9	769.9	414.8	590.5	435.4
Muscle	30.5	23.2	42.2	16.5	7.7	25.8	17.0	14.2	22.1
Plasma	5.0	10.0	6.7	9.3	5.5	6.8	7.7	8.9	7.5
Terminal Bladder Urine	261.6	685.7	429.3	505.1	++	388.0	904.8	695.5	552.8
Body Temperature at Sacrifice °C	17.6	17.6	19.2	22.6	29.0	33.0	34.0	35.2	26.0

++= No Sample Available

3

UREA CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

Group I WINTER TORPID ANIMALS

mM/l

Prairie Dog No./Sex	18-♀	19-♀	20-♀	21-♂	22-♂	Mean
C1	13.9	10.3	19.1	27.8	12.8	16.8
C2	13.4	10.6	30.4	31.2	11.6	19.4
OZ	17.4	10.4	32.3	35.2	18.9	22.8
IZ1	19.3	11.8	33.2	37.4	22.4	24.8
IZ2	21.2	13.4	34.3	61.0	18.9	29.7
Muscle	13.9	14.0	++	21.3	7.9	14.3
Plasma	6.2	5.9	7.2	6.1	6.5	6.4
Terminal Bladder Urine	361.8	473.8	518.6	313.0	275.4	388.5
Body Temperature at Sacrifice °C	12.4	11.0	13.8	14.2	11.1	12.5

++ = No Sample Available

4

UREA TF/P, U/P, AND M/P RATIOS

Group III ANIMALS

Kidney TF/P

Prairie Dog No.	13	14	12	16	15	17	Mean
C1	5.3	3.2	1.7	2.0	3.3	2.7	3.0
C2	5.9	8.4	8.4	2.9	11.2	6.6	7.2
OZ	31.8	39.8	26.6	20.4	37.9	23.1	29.9
IZ1	42.2	62.1	38.4	27.3	54.9	36.2	43.5
IZ2	52.9	63.1	57.0	30.5	58.7	54.9	43.0
U/P (Terminal Bladder Urine)	126.8	109.8	85.4	62.8	77.2	82.4	90.7
M/P	5.2	3.0	1.7	2.0	2.9	2.5	2.9

UREA TF/P, U/P, AND M/P RATIOS

Group II ANIMALS

Kidney TF/P

Prairie Dog No.	5	10	2	1	4	8	7	6	Mean
C1	12.8	2.3	5.3	2.5	1.8	2.9	2.4	3.5	4.2
C2	12.3	9.9	19.9	7.2	2.8	11.6	6.0	3.1	9.1
OZ	30.1	25.9	40.6	29.2	16.8	50.5	20.5	18.0	28.9
IZ1	36.0	++	48.9	30.3	19.7	85.4	41.7	43.1	38.1
IZ2	39.8	61.3	65.7	35.5	22.7	113.2	53.8	66.3	57.3
U/P (Terminal Bladder Urine)	52.3	68.5	64.0	54.3	++	57.0	117.5	78.1	70.1
M/P	6.1	2.3	6.3	1.7	1.4	3.8	2.2	1.6	3.1

++ = No Sample Available

UREA TF/P, U/P, AND M/P RATIOS

Group I ANIMALS

Kidney TF/P Prairie Dog No.	18	19	20	21	22	Mean
C1	2.2	1.7	2.6	4.5	1.9	2.6
C2	2.1	1.8	4.2	5.1	1.8	3.0
O2	2.8	1.7	4.5	5.7	2.9	3.5
IZ1	3.1	2.0	4.6	6.1	3.4	3.8
IZ2	3.4	2.2	4.7	10.0	2.9	4.6
U/P (Terminal Bladder Urine)	58.3	80.3	72.0	51.3	42.3	60.8
M/P	2.2	2.3	++	3.5	1.2	2.3

++ = No Sample Available

7

SODIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

GROUP III ANIMALS

mEq/l

Prairie Dog No.	13	14	12	16	15	17	Mean
C1	80.1	47.6	32.6	56.1	51.8	61.2	54.9
C2	97.1	66.0	87.8	61.7	94.5	85.8	82.1
OZ	243.9	140.8	130.0	162.3	126.0	137.9	156.8
IZ1	297.0	171.8	192.8	185.4	177.2	183.1	201.2
IZ2	330.2	236.0	212.0	204.5	183.0	288.6	242.4
Muscle	50.7	32.6	22.3	26.3	28.1	46.0	34.3
Plasma	155.7	155.2	158.7	155.4	152.0	158.9	156.0
Terminal Bladder Urine	100.8	102.1	100.0	++	11.7	16.8	66.3

++ = No Sample Available

8 SODIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

GROUP II ANIMALS

mEq/l

Prairie Dog No.	5	10	1	2	4	8	7	6	Mean
C1	82.9	65.1	61.3	100.3	34.7	34.6	56.0	65.9	62.6
C2	190.0	98.0	75.0	232.8	60.0	98.9	104.3	76.8	116.7
OZ	273.2	165.0	271.0	374.8	160.0	187.6	175.5	154.8	220.2
IZ1	396.7	211.7	340.6	383.8	187.0	221.7	218.9	222.5	272.8
IZ2	427.0	302.0	375.6	430.0	231.0	374.0	268.5	303.5	338.9
Muscle	39.3	54.3	42.0	66.1	25.5	26.7	34.4	34.6	40.3
Plasma	128.2	135.0	131.5	132.6	136.9	135.8	159.0	152.0	138.8
Terminal Bladder Urine	-0-	95.1	11.4	87.5	++	10.3	125.0	21.7	50.1

++ = No Sample Available

9

SODIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

GROUP I ANIMALS

mEq/l

Prairie Dog No.	18	19	20	21	22	Mean
Cl	84.8	59.0	67.3	58.4	66.0	67.1
C2	79.4	57.6	72.9	56.0	67.0	66.6
OZ	83.1	63.1	74.0	69.5	77.0	73.3
IZ1	87.0	67.0	71.1	81.0	79.0	77.0
IZ2	94.0	81.0	80.0	97.0	80.9	86.6
Muscle	69.0	45.4	++	43.3	33.0	47.6
Plasma	138.0	146.0	145.0	145.6	141.5	143.2
Terminal Bladder Urine	24.5	27.7	86.4	8.2	27.1	34.7

++ = No Sample Available

SODIUM TF/M AND P/M RATIOS

GROUP III ANIMALS

Prairie Dog No.	13	14	12	16	15	17	Mean
C1	1.6	1.4	1.4	2.1	1.8	1.3	1.6
C2	1.9	2.0	3.9	2.3	3.3	1.8	2.5
OZ	4.8	4.3	5.8	6.1	4.5	3.0	4.7
IZ1	5.8	5.2	8.6	7.0	6.3	3.9	6.1
IZ2	6.5	7.2	9.5	7.7	6.5	6.2	7.2
P/M	3.0	4.7	7.1	5.9	5.4	3.4	4.9

SODIUM TF/M AND P/M RATIOS

GROUP II ANIMALS

Prairie Dog No.	5	10	1	2	4	8	7	6	Mean
C1	2.1	1.2	1.4	1.5	1.3	1.3	1.6	1.9	1.5
C2	4.8	1.8	1.8	3.5	2.3	3.7	3.0	2.2	2.9
OZ	6.9	3.0	6.4	5.6	6.2	7.0	5.1	4.5	5.6
IZ1	10.0	3.9	8.1	5.8	7.3	8.3	6.3	6.4	7.0
IZ2	10.8	5.5	8.9	6.5	9.0	14.0	7.8	8.7	8.9
P/M	3.2	2.5	3.1	2.0	5.3	5.0	4.6	4.4	3.7

11

SODIUM TF/M AND P/M RATIOS

GROUP I ANIMALS

Prairie Dog No.	18	19	20	21	22	Mean
C1	1.2	1.3	1.4	1.3	2.0	1.4
C2	1.1	1.2	1.5	1.3	2.0	1.4
OZ	1.2	1.4	1.5	1.6	2.3	1.6
IZ1	1.2	1.4	1.5	1.8	2.4	1.6
IZ2	1.3	1.8	1.7	2.2	2.4	1.8
P/M	2.0	3.2	3.0	3.3	4.3	3.1

13 POTASSIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

GROUP III ANIMALS

mEq/l

Prairie Dog No.	13	14	12	16	15	17	Mean
C1	50.6	60.5	70.5	69.8	71.1	73.8	66.0
C2	55.5	51.3	69.9	68.6	73.0	75.7	65.6
OZ	58.8	63.2	68.7	64.7	71.9	62.5	64.9
IZ1	55.7	65.0	66.1	74.9	70.3	60.3	65.4
IZ2	++	++	++	++	++	71.3	71.3
Muscle	105.1	102.0	112.8	115.6	103.7	127.5	111.1
Plasma	9.2	7.5	7.6	9.6	6.9	7.5	8.0
Terminal Bladder Urine	181.0	181.6	165.0	++	127.8	167.5	164.6

++ = No Sample Available

14 POTASSIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

GROUP II ANIMALS

mEq/l

Prairie Dog No.	5	10	1	2	4	8	7	6	Mean
C1	83.6	61.2	86.5	115.0	63.2	61.9	75.0	75.3	77.7
C2	83.0	61.9	87.5	116.8	65.1	56.9	74.6	74.6	77.5
OZ	84.7	60.3	++	114.0	64.3	59.9	72.3	76.6	76.0
IZ1	95.0	66.0	84.3	117.0	62.4	58.1	71.6	79.8	79.3
IZ2	85.0	++	++	++	++	++	71.2	79.6	78.6
Muscle	88.0	96.0	116.8	119.0	126.3	112.0	115.4	97.3	108.8
Plasma	11.4	6.4	4.6	6.4	13.4	10.5	7.9	9.5	8.7
Terminal Bladder Urine	40.6	64.5	62.6	13.1	++	97.2	++	52.4	55.0

++ = No Sample Available

POTASSIUM CONCENTRATIONS IN RENAL TISSUE SLICES, PLASMA AND URINE

<u>GROUP I ANIMALS</u>

mEq/l

Prairie Dog No.	18	19	20	21	22	Mean
Cl	74.8	91.0	74.8	78.3	++	79.7
C2	64.4	87.0	71.4	77.2	73.2	74.6
OZ	70.0	89.4	71.6	75.6	72.9	75.9
IZl	74.2	88.6	70.6	76.9	69.7	76.0
IZ2	71.7	85.4	68.5	74.1	++	74.9
Muscle	132.6	134.0	++	121.0	105.0	123.1
Plasma	7.3	8.0	5.4	7.5	9.5	7.5
Terminal Bladder Urine	57.5	73.5	89.8	68.4	19.2	61.7

++ = No Sample Available

POTASSIUM TF/P, U/P AND M/P RATIOS

GROUP III ANIMALS

Prairie Dog No.	13	14	12	16	15	17	Mean
C1	5.5	8.0	9.2	7.3	10.3	9.8	8.3
C2	6.0	6.8	9.2	7.1	10.5	10.0	8.3
OZ	6.4	8.4	9.0	6.7	10.4	8.3	8.2
IZ1	6.0	8.6	8.7	7.8	10.2	8.0	8.2
IZ2	++	++	++	++	++	9.5	—
Terminal U/P	19.6	24.2	21.7	++	18.5	22.3	21.2
M/P	11.4	13.6	14.8	12.0	15.0	17.0	13.9

++ = No Sample Available

16

POTASSIUM TF/P, U/P AND M/P RATIOS

GROUP II ANIMALS

Prairie Dog No.	5	10	1	2	4	8	7	6	Mean
C1	7.3	9.5	18.8	17.9	4.7	5.9	9.5	7.9	10.2
C2	7.3	9.6	19.0	18.2	4.8	5.4	9.4	7.8	10.2
OZ	7.4	9.4	++	17.8	4.8	5.7	9.1	8.0	8.9
IZ1	8.3	10.3	18.3	18.3	4.6	5.5	9.0	8.4	10.3
IZ2	7.4	++	++	++	++	++	9.0	8.3	8.2
Terminal U/P	3.5	10.0	13.6	2.0	++	9.2	++	10.2	8.0
	7.7	15.0	25.4	18.5	9.4	10.6	14.6	5.5	13.3

++ = No Sample Available

18

POTASSIUM TF/P, U/P AND MUSCLE/P RATIOS

GROUP I ANIMALS

Prairie Dog No.	18	19	20	21	22	Mean
C1	10.2	11.3	13.8	10.4	++	11.4
C2	8.8	10.8	13.2	10.3	7.7	10.2
OZ	9.6	11.1	13.2	10.1	7.7	10.3
IZ1	10.1	11.0	13.0	10.2	7.3	10.3
IZ2	9.8	10.6	12.7	9.9	++	10.7
Terminal U/P	7.8	9.2	16.6	9.1	2.0	8.9
M/P	18.1	16.8	++	16.1	11.0	15.5

++ = No Sample Available