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THE EFFECT OF COLD EXPOSURE ON THE
SODIUM AND WATER BALANCE OF THE
PORCUPINE, <u>ERETHIZON</u> <u>DORSATUM</u>

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Stephen Paul Rogers

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Richard W. Hill
Major professor

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THE EFFECT OF COLD EXPOSURE ON THE SODIUM AND WATER BALANCE OF THE PORCUPINE, *ERETHIZON DORSATUM*

By

Stephen Paul Rogers

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ABSTRACT

THE EFFECT OF COLD EXPOSURE ON THE SODIUM AND WATER BALANCE OF THE PORCUPINE, *ERETHIZON DORSATUM*

By

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The impact of winter on the sodium and water balance in the porcupine was evaluated by the collection of animals prior to winter (November) and in late winter (March), and subsequent analysis of various body parameters. Serum sodium concentration in juveniles and pregnant females were seen to decrease by late winter, although adult males maintained serum sodium to be within normal mammalian physiological limits. This, along with a net increase in sodium retention via the fecal and urinary routes, suggested that some factor was responsible for increased sodium stress during the interim. Analysis of porcupine winter foods, combined with a separate laboratory study, indicate that sodium levels in the natural foods were adequate to maintain a net sodium balance. In response to winter, porcupines were found to increase the relative medullary thickness of the kidney, increase urine osmolality and decrease fecal water content. This indicated that the porcupines were probably either undergoing water stress or using these means to decrease water turnover rate.

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I especially thank my father who was my able field assistant and guide through all phases of my field work, and to my mother who didn't get too upset about finding porcupine quills in the living room. And lastly, I am indebted to that furry little ball of quills called the porcupine.

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INTRODUCTION

The survival of a mammal in the natural environment is dependent on its ability to maintain itself against environmentally adverse conditions. One such condition inherent to herbivorous mammals is that of limitation of sodium. In general, terrestrial plants do not require or accumulate sodium (Epstein 1972). Passive movement of sodium into vegetation is often limited in regions where rainfall continuously leaches sodium from the soil and litterfall. Many terrestrial environments throughout the world have so little sodium that this ion may actually be a limiting factor to mammalian population size (Aumann 1965, Blair-West et al. 1968, Jordan et al. 1973, Belovsky 1978).

Animals deficient in sodium have been shown to seek the ion actively. Deficient domestic and laboratory animals select specifically for sodium (Denton and Sabine 1961) and have been shown to ingest proper quantities to regain sodium balance (Novakova and Cort 1966). Herbivores often search out mineral licks, apparently to obtain necessary amounts of dietary minerals, primarily sodium (Weeks 1978).

A seasonal spring peak in sodium appetite has been noted in a wide variety of herbivorous mammals: elk (Dalke et al. 1965, Knight and Mudge 1967), deer (Weeks and Kirkpatrick 1976), mountain goats (Hebert and Cowan 1971), moose (Botkin et al. 1973, Jordan et al. 1973), rabbits (Blair-West et al. 1968), porcupines (Campbell and LaVoie 1967), woodchucks and fox squirrels (Weeks and Kirkpatrick 1978).

The salt appetite noted is common to all ages and sexes, although it is undoubtedly influenced by pregnancy and/or lactation.

Various explanations to account for this seasonality of sodium appetite are all based on studies conducted on domestic animals. Frens (1958) has shown that a diet of new growth grass increased the fecal loss of sodium by cattle to a point where symptoms of sodium deficiency were detected. Suttle and Field (1967) working with sheep found that increased potassium content of forage and increased water intake could lead to sodium deficiency. These two factors have been repeatably cited to explain the spring peak in sodium appetite (Blair-West _et_ _al_. 1968, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976).

An additional factor, which at this time has not yet been implicated in seasonal salt balance, is the effect of winter cold. Laboratory studies have shown cold exposure to have profound effects on salt and water balance. Fregley (1968), working with rats, found that exposure to cold for 10 days resulted in dehydration of the body, coupled with a net loss of sodium and potassium. Identical results were observed by Neff (1966) in chipmunks. Ringens _et_ _al_. (1977) also noted a cold diuresis in tundra voles, but failed to measure sodium balance. In rats, dehydration appears to be maintained for as long as the animal remains in the cold conditions (Box _et_ _al_. 1973, Fregly _et_ _al_. 1976). Field studies of seasonal body water composition in shrews (Myrcha 1969) and black-tailed deer (Longhurst _et_ _al_. 1970) corroborate these data.

The literature is fairly confusing on the effects of cold exposure on the sodium concentration of body tissues. Only three publications could be found addressing this subject. Clausen and

Storesund (1970) studying hibernating hedgehogs found a significant decrease in sodium concentration in liver and heart tissue, but a non-significant decrease in skeletal muscle. Yunosov and Gitel'man (1973) studied the effect of different environment temperatures on the redistribution of potassium and sodium in rat tissues. At an environmental temperature of 0-5° C the quantity of sodium in the majority of tissues dropped by 24.6-41.1%, but potassium changed little. Smith et al. (1978) found a significantly elevated sodium concentration in thigh muscle in winter-collected yearling male and juvenile and adult female snowshoe hares, versus those collected in summer at a time of sodium stress.

Three possible explanations can be proposed to explain a loss of sodium as a result of cold exposure. First, dehydration in itself would cause sodium loss, assuming that the sodium concentrations of tissues and body fluids remain at fixed physiological levels. Rehydration results in sodium appetite when the animal attempts to restore the sodium required to maintain homeostasis (Fitzsimmons 1975).

The use of the sodium pump has recently been shown to be an important means of elevating heat production in non-shivering thermogenesis of a variety of tissues (Ismail-Beigi and Endelman 1970, Horwitz 1973, Stevens and Kido 1974, Horwitz and Eaton 1977, Asano et al. 1976, Guernsey and Stevens 1977). The present belief concerning thermogenesis by active sodium transport is based on the hypothesis that, by some means, the membranes of the cells are made leaky to sodium and ATP is consumed in a futile cycle by pumping sodium to maintain the normal concentration gradient. There may be a possible repercussion in utilization of this cycle leading to a net loss of sodium from the body.

Third, the stress of winter may be sufficient to complicate sodium retention abilities. It has been shown in voles (Aumann and Emlen 1965) that stress from increased population density influenced the various zones of the adrenal glands in such a way as to increase sodium loss from the body and increase sodium appetite. Cold exposure may affect the zones of the adrenal glands or other sites in the body important to sodium balance.

The general aim of the present study is to determine the effect that cold exposure and natural winter conditions have on the salt balance of a mammal. To my knowledge, this is the first study of this kind to combine field measurements with a simultaneous laboratory study. It was felt that documentation of the disturbances of salt and water balance resulting from cold exposure would shed light on overall yearly sodium balance.

The animal chosen for this study was the American porcupine, *Erethizon dorsatum*, for the following reasons. Most previous laboratory studies on sodium and water balance have been done on rodents. Porcupines are strict herbivores, their winter food habits are well documented, and they are noted throughout the continent for an intense craving for salt. They also appear to be cold stressed in winter (Clarke and Brander 1973). Ease of collection, size, and apparent ability to adjust to laboratory confinement (Bloom *et al*. 1973) also entered into this decision.

The specific aims of the present study may be stated as follows:

1. To determine the effect that the natural winter environment has on the primary routes important to sodium balance.

Measured were: kidney size and concentrating ability, urine osmolality and sodium and potassium concentration, and fecal moisture and cation concentrations.

2. To determine effects of winter on the sodium and potassium concentration of blood serum, liver and skeletal muscle.
3. To determine the effect of cold exposure in the laboratory on overall sodium balance in the porcupine, and to assess this influence on the above mentioned body parameters.

MATERIALS AND METHODS

The investigation had two divisions. A field study was conducted which involved measurements of various body parameters of wild-collected porcupines at two times of the year, prior to initiation of winter (November 10-25) and late winter (March 2-15). Second, a laboratory study was performed on the effects of cold exposure on salt balance. Porcupines for this study were collected at the beginning of winter (December 21-23) and divided into two groups, the members of which were housed individually in outdoor and indoor enclosures, respectively. They were allowed to adjust to captivity for five weeks, after which precise measurements were taken on sodium balance of each animal for a 22-24 day period. At the completion of this monitoring period, the animals were autopsied and measured for the same parameters as in the field study.

Description of Study Area

The field portion of this study was conducted on the Wilcox Unit of Armstrong Forest Lands (division of Texas Gulf Sulphur Company) in Elk and McKean counties of northwest-central Pennsylvania (see Figure 1). This region falls within the high Allegheny Plateau discussed by Hough and Forbes (1943). These forests were harvested around the turn of the century, and since then have progressed to a mature second growth forest, primarily composed of beech, maple, hemlock and black cherry. Hemlock is generally confined to creek bottoms, wet areas,

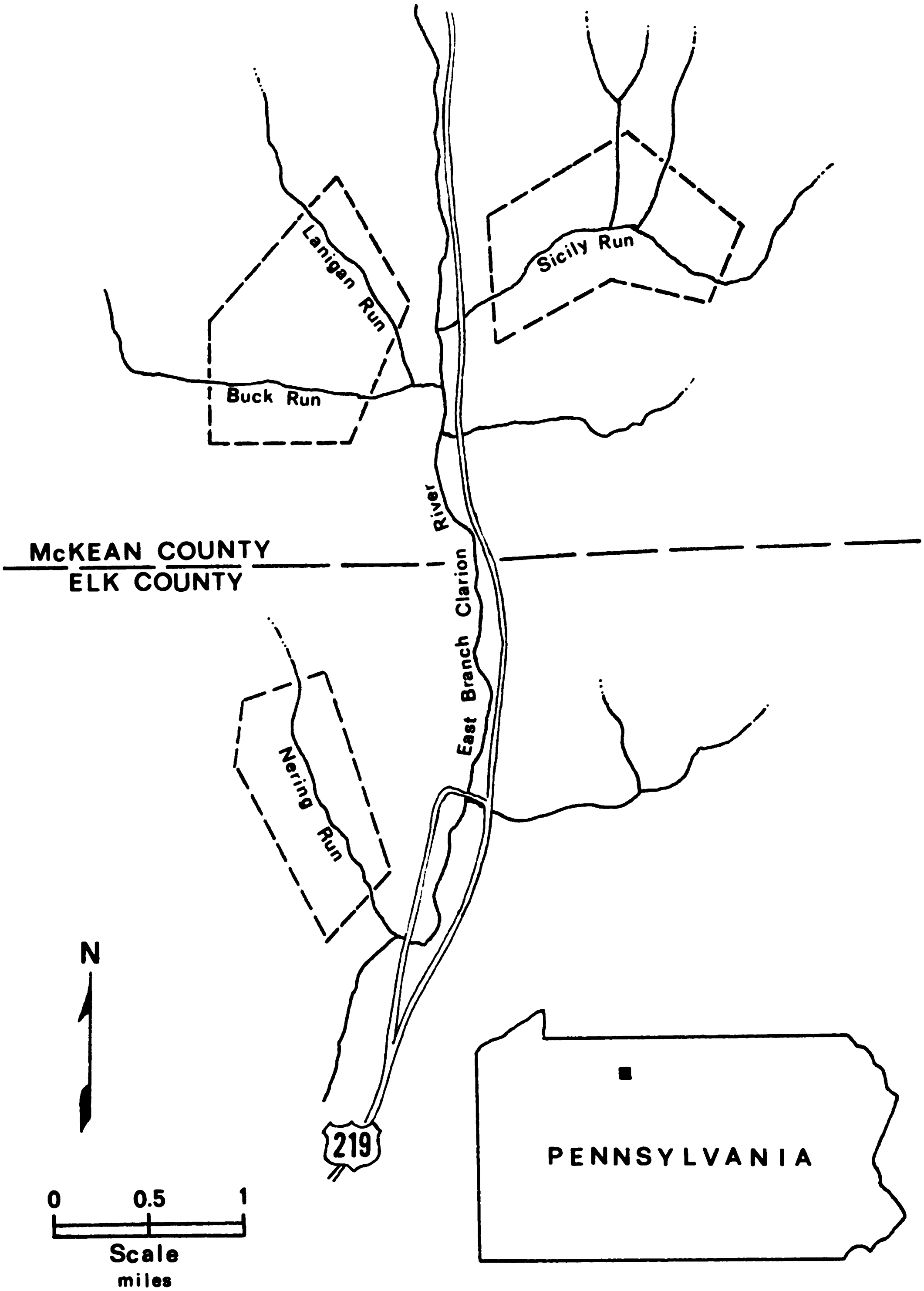

Figure 1. Porcupine field study area.

and north and east slopes. Porcupines abound on the study site. Despite persecution and slaughter by local foresters, lumberman, trappers and hunters, the porcupine hold their own and were present during this study in populations estimated to be 30-40 animals per square mile.

The laboratory animals were collected on areas approximately 15-20 miles southwest of the study site used in the field investigation. The area used falls within State Game Lands no. 44 in central Elk County. See Figure 2. The two study sites were sufficiently close for the porcupines to be considered parts of the same breeding population (George M. Kelly, personal communication). Separate field and laboratory sites were required because of the living habits of the porcupine. The laboratory-site animals resided in dens along dissociated rock outcrops. Nightly foraging trips from the dens were taken to and from feeding areas. Once an animal was tracked to its denning site, it could readily be caught in a leghold trap when it came out for the following night's activities. Porcupines on the field site resided in station trees throughout the year. This allowed daylight collection but prevented live trapping.

Field Study Methods

Porcupines were collected for field study with a twenty gauge shotgun between the hours of 9:00 AM and 3:00 PM EST. Most animals collected in this manner were killed instantly. A total of 16 animals was collected in November (4 juveniles, 6 pregnant females, 6 adult males) and 19 porcupines in March (7 juveniles, 6 pregnant females, 1 non-pregnant female, 5 adult males). A thorough autopsy was preformed on each animal.

Immediately following death a blood sample was taken from each

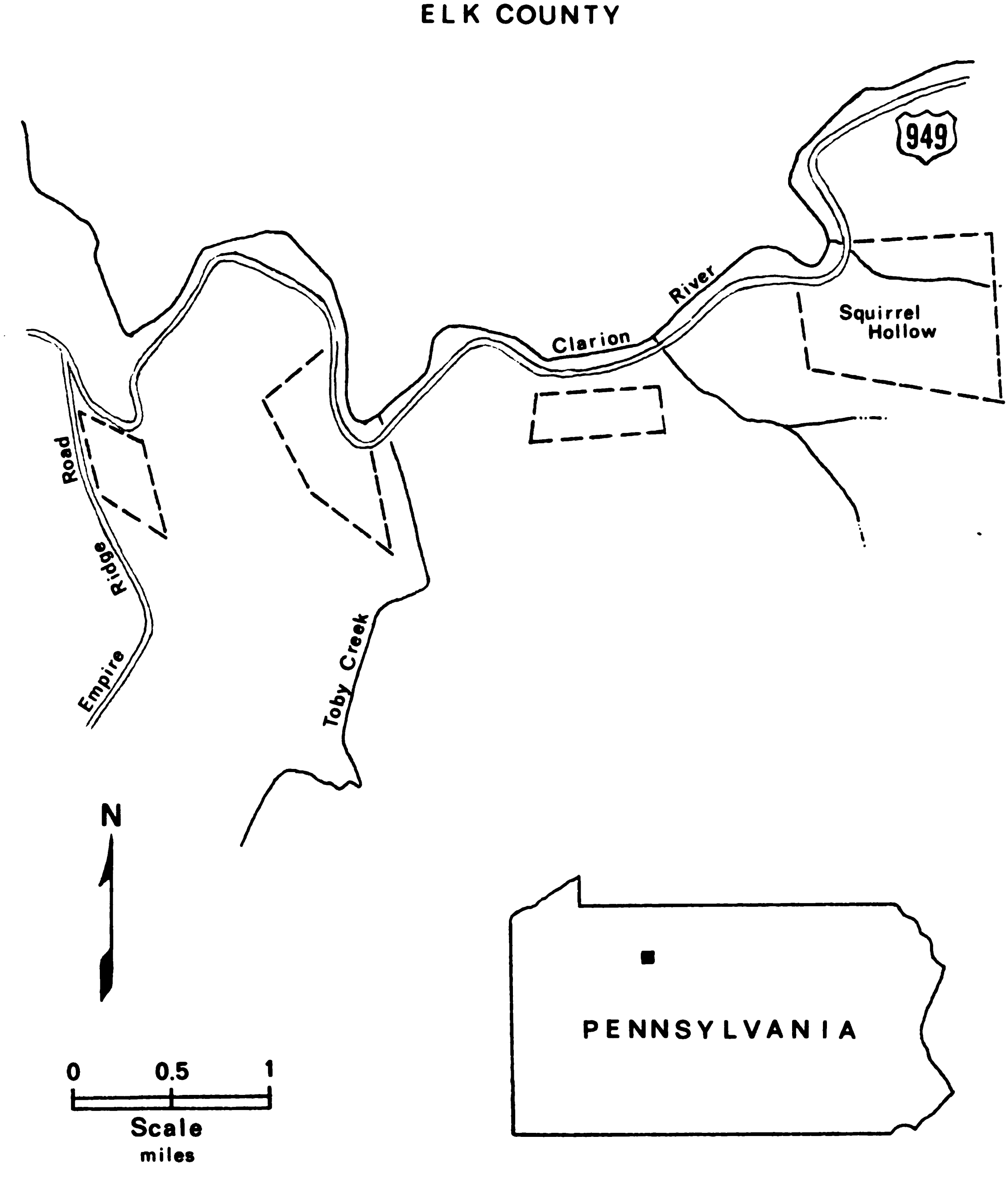

Figure 2. Laboratory animal collection site.

porcupine by deeply slicing the throat region with a five-inch stainless steel skinning knife (R. H. Forschner Co. Switzerland). The blood flowed freely and was collected directly in three to six serological test tubes. During initial coagulation the clot was loosened from the wall by use of a nichrome innoculating needle. The sample was then left undisturbed to continue clotting. After a period of approximately 10 minutes, a clear serum supernatent appeared. This liquid was poured off into a plastic vial, sealed with Scotch plastic electrician tape no. 88, and frozen for later analysis. Serum sodium and potassium concentrations were measured using a Model 143 Flame Photometer (Instrumentation Laboratories Inc, Boston) with lithium as an internal standard.

Simultaneous to the collection of the blood in the serological tubes, a sample was collected for micro-hematocrit measurement by use of Red Tip no. 2629-B Heparinized Capillary Tubes (Sherwood Medical Industries Inc.). Three to five tubes were collected from each animal, packed in clay, and prevented from being frozen in the field. The tubes were then centrifuged at 2000 rpm and the packed cell volume (PCV) noted. This speed was sufficient to pack the cells thoroughly, and duplicate readings were usually recorded from the same animal. When PCV readings varied slightly, they were averaged.

Gross body data obtained at autopsy included the typical mammalian museum measurements, i.e. sex and reproductive status, total length, tail length, right ear and foot length, and total weight. The skull from each porcupine was cleaned, aged using criteria of Dodge (1967) and Earle (1978), and preserved in the MSU Museum at East Lansing (catalogue nos. 33032-33087).

Urine was collected directly from the bladder by use of a disposable plastic syringe. For storage, it was placed in a plastic vial, sealed with tape and frozen until analysis. Sodium and potassium concentrations were measured on the Model 143 Flame Photometer. Because sodium concentrations were low, an initial dilution of only one to ten was required to measure this ion accurately. This solution was diluted additionally to obtain a reading on potassium. Osmolality of the urine was assessed with a Wescor Model 5100-A Vapor pressure Osmometer. Readings were taken on all samples at one time to minimize machine fluctuations and human error.

Data obtained from the kidneys included relative medullary thickness (RMT), weight and moisture content. In the field the left kidney was utilized in measurement of RMT. This index to the renal concentrating ability of the kidney was developed by Sperber in 1944, and is defined as:

$$\text{RMT} = 10\ (r)\ [(t)\ (h)\ (l)]^{-\,0.33}$$

where t represents kidney thickness, h is height, l equals length, and r stands for the radial extension of the medulla. The gross dimensions of the kidney were obtained using a finely calibrated ruler. The kidney was then exposed by making a careful mid-sagittal cut with a sharp knife such that the maximum area of the medulla from the cortical-medullary boundary to the tip of the renal papilla was visible. Five measurements from the renal papilla to the cortical-medullary boundary were recorded and averaged to obtained the radial extension of the medulla. After these measurements were taken, the kidney was placed in a pre-weighed vial, later weighed and stored frozen. At a later time the moisture content was determined on this sample by drying to constant weight at 60° C (Napco Model 620 drying oven).

During autopsy the right kidney was excised and placed in AFA reagent (10% formaldehyde, 10% glacial acetic acid, 30% ethyl alcohol and 50% distilled water). It was anticipated that only a small difference in the RMT measurements might occur in the field-measured kidneys from the fall and late winter periods, in which case the fixed tissues were to be sliced with more precision in the laboratory with a microtome. However, examination of the data at the end of the field study indicated that a significant difference did occur between fall and late winter kidneys sectioned by hand. Therefore the fixed kidney of each porcupine was used to obtain a second measurement of RMT for each animal by hand methods and the values averaged.

The liver was excised during autopsy and placed in a pre-weighed ziplock bag. After return from a field day, the liver samples were weighed, all air was squeezed out, each bag was sealed in two additional heavy-duty plastic bags, and stored frozen. Sodium and potassium concentrations were measured on a cubic centimeter section of the tissue weighing approximately one gram, which was cut from the central core of the liver. The sample was wet-ashed overnight in concentrated reagent-grade nitric acid and diluted appropriately to obtain readings on the ions. Moisture content was measured on a one-centimeter-thick central slice cut through the dorso-ventral plane of the liver.

Skeletal muscle tissue was analyzed in much the same manner as liver. During autopsy a sample of skeletal muscle was collected from the upper thigh. All fat was trimmed off and the sample stored frozen in a vial. A one-cubic-centimeter subsample was utilized to obtain ion concentrations by wet ashing. Moisture content was measured on the remaining tissue.

During autopsy fecal samples were collected directly from the large intestine. This was accomplished by severing the distal end of the colon and squeezing out a number of fecal pellets into a pre-weighed vial. The vial was then sealed and frozen until later analysis. Each sample was dried at 80° C to constant weight to obtain moisture content. Approximately two grams of the dried sample were placed in a clean Coors crucible, placed in a cold muffle furnace, brought slowly to 500° C and ashed for two hours. After cooling, 10 ml of 6 molar HCl was added to the crucible containing the ash, heated to 100° C for 10 minutes, and filtered through a Whatman no. 42 filter paper into a 100 ml volumetric flask. The crucible and filtering apparatus were rinsed three times and the washings added to the flask, which was then brought to volume. From the resulting solution sodium could be measured directly with the flame photometer, but a second dilution was required to read potassium.

An additional factor important to the annual sodium balance of a female is the loss of sodium due to reproduction. In order to obtain a rough estimate of this loss, three fetuses and one placental complex were collected from the late winter period. These samples were cut at the umbilical cord and stored frozen within three layers of plastic bags. For analysis the materials were cut into smaller pieces and homogenized for five minutes in a clean Waring blender. A 15-gram subsample was extracted, placed on a disposable plastic petri plate and dried at 60° C for 48 hours to obtain average body moisture.

Two grams of this dried sample were ashed for three hours at 550° C in a Coors crucible, dissolved in 15 ml 6 molar HCl and diluted to 1 liter. Sodium and potassium levels were obtained on this solution. Amniotic fluid from four porcupines was also analyzed for these ions.

All field specimens were roughly examined to estimate their parasitic tapeworm and roundworm levels. This was accomplished by a visual inspection of the intestinal contents. Two samples of tapeworms, approximately 20, probably Monoecocestus, were collected for sodium determination of the dried samples. Because of the small size of the abundant nematodal parasite, probably Wellcomia, and difficulty in separation from intestinal contents, no ion determinations were attempted.

Thirteen major food plant species were collected in the fall and winter periods. Bark tissue was collected from areas adjacent to recent feeding, by slicing bark with a stainless steel knife to fall directly into a plastic bag which was used in frozen storage. Hemlock foliage was sampled by collecting needles from branches in close proximity to those which had been clipped and the needles consumed, or by removing the few needles remaining on the fallen branches. Ash and sodium and potassium concentrations were analyzed in the same manner as fecal samples. Food species being utilized by each animal was noted by visual observation, but no attempt was made to quantify amounts of foods ingested on a daily basis.

Laboratory Study

Porcupines used in the laboratory study were collected by use of no. 1 1/2 and no. 2 Victor coilspring steel leghold traps. Initially smaller traps had been tested, but these were found to be incapable of holding the porcupines. Transport of the mammals from the trap site to a waiting vehicle was accomplished by use of a holding cage (50 cm x 50 cm x 32 cm, weight 14 kg) strapped to a backpack frame. In the case of there being two or more animals on a given trapping circuit, the additional porcupines were carefully placed in burlap bags for transfer. Even 9 kilogram specimens were transferred by this latter method, although with extreme difficulty.

The laboratory facility used in this study allowed porcupines to be maintained in two adjacent rooms under different temperature conditions. One half of the animals were kept inside under controlled temperature ($18 \pm 3°$ C) and lighting (a 150 Watt flood lamp was manually controlled to natural daylength). A second group was housed in an outside enclosure which was open to the sky so that they encountered winter conditions. Temperature was monitored with a Taylor maximum-minimum thermometer.

All porcupines were housed individually in stainless steel cages, 90 cm x 60 cm x 32 cm (Unifab Corporation, Kalamazoo Michigan). Food and water were provided ad lib. in stainless steel bowls (11 cm in diameter and 8 cm deep). The food diet provided was modeled after a low sodium mixture formulated by Grace, et al. (1979). The sodium concentration approximated the level found in the natural winter foods. The diet contained: 35% soybean meal, 30% coarse ground corn, 12% alfalfa meal, 12% coarse ground oats, 5% wheat bran, 5% corn oil, 1% $CaCO_3$, 0.6% vitamin D, 0.1% methionine and 0.025% vitamin A. Water was changed daily for the inside animals to prevent microbial growth. Outside water containers were changed twice daily to allow access to liquid water in the subfreezing temperatures.

After a five-week period of adjustment, the flow of sodium through each porcupine was monitored for 22 to 24 days. This was accomplished by careful measurements on food consumption, and feces and urine production and sodium concentration. Porcupines were supported on coarse screen which permitted passage of fecal pellets and urine to a stainless steel pan below. Urine was collected under mineral oil for the inside animals. In the outdoor enclosure, urine was allowed to freeze in the bottom of the pan and was thawed to obtain urine production data. Tests with control pans showed very little deliquescence to occur, and absolute values of sodium were unchanged. On a daily basis approximately 30 ml of urine and 15 grams of feces from each animal were sampled, sealed in vials and stored frozen. Sodium concentration was determined on these samples. Fecal moisture obtained on the subsamples was used to correct to dry feces production per day.

From the beginning the laboratory study was beset with problems. During capture of the first porcupine on December 21, one of the author's fingers was broken. This severely hampered field operations, which only succeeded due to help of the author's father. After two additional trap nights the snow cover melted which made further trapping unprofitable. Fifteen animals were collected in the three-day trapping period but one escaped on Christmas eve. During transport of the animals to Michigan on Christmas Day, the fuel pump of the vehicle failed, forcing an unscheduled layover in Cleveland. This was probably most important because of the additional stress placed on the animals. After final transfer of the porcupines to Michigan State, one died of natural causes within two days and a second was dispatched because of a severe mange infection. Division of the remaining 12 animals left six in each temperature regime. They were slowly adjusted from a diet of acorns obtained from the laboratory site to the artificial diet. Conversion required four weeks for eight animals, but the remaining animals never adjusted and ate no food diet during the entire study. Unfortunately, all four of these animals were from those maintained inside, leaving two as a sample size for this temperature condition. Following completion of the monitoring period all porcupines were autopsied in the same manner as in the field study. Frozen samples from the autopsy were lost in a freezer malfunction.

As a result of the setbacks, the only information obtained from the laboratory study was: 1) Complete salt balance data for eight porcupines - six maintained outside, two maintained inside. 2) Data obtained during autopsy - organ weights, RMT values, and hematocrit.

Statistical procedures involved use of the Student's t test to evaluate differences between means.

RESULTS
AND
PRELIMINARY DISCUSSION

Porcupines on the field study site consumed a wide variety of tree barks during the fall, but by late winter generally restricted their diet to hemlock with only an occasional deciduous tree. The importance of hemlock in winter food consumption has been noted in a number of studies conducted in the hardwood-hemlock forests of the northeast (Curtis and Kozicky 1944, Shapiro 1949, Dodge 1967, Brander 1973, Earle 1978 and Kelly 1979). Hemlock is the preferred station tree (Curtis and Kozicky 1944), and the majority of the porcupines were collected from this species, 75% of the fall animals and 95% in winter. However, it was evident in the fall that porcupines would feed on adjacent deciduous trees as well as the hemlock in which they resided. During winter they often remain in the same hemlock for a week, even up to a month (Silve, personal communication), feeding solely on this food source. This shifting to hemlock may be a result of the food quality value of that species (see Gill and Cordes 1972, for a discussion of porcupine food quality evaluation), or it may be due to difficulty of snow travel coupled with the energy savings of being stranded in an evergreen versus a deciduous tree (Clarke and Brander 1973).

Data obtained from the vegetation analysis appear in Table 1. Sodium concentrations in bark tissues remain constant on a seasonal basis (Likens and Bormann 1970, Day and Monk 1977), so data from fall

Table 1. Sodium and potassium concentrations of vegetation samples collected from the field and laboratory sites.

Species	Sample	n	Na^+ mequiv/kg dry wt. ($\bar{x} \pm SE$)	K^+ mequiv/kg dry wt. ($\bar{x} \pm SE$)	K^+: Na^+
Tsuga canadensis	needles	4	9.42 ± 1.53	133.77 ± 12.4	14.20:1
" "	bark	1	2.72	33.22	12.23:1
" "	root bark	1	5.56	36.69	6.60:1
Fagus grandifolia	bark	4	4.33 ± 0.32	36.13 ± 5.44	8.34:1
Prunus serotina	bark	1	7.27	58.43	8.04:1
Prunus pennsylvanica	bark	1	5.76	34.37	5.97:1
Betula lenta	bark	1	5.66	114.30	20.19:1
Betula alleghaniensis	bark	1	3.58	59.65	16.66:1
Acer saccharum	bark	1	5.36	57.02	9.34:1
Acer rubrum	bark	1	12.41	60.61	4.88:1
Hamamelis virginiana	bark	1	10.96	57.02	5.20:1
Aralia spinosa	bark	1	5.92	38.05	6.43:1
Quercus rubra*	acorns	1	1.25	263.10	210.48:1
Quercus velutina*	acorns	1	0.90	179.71	199.70:1
Dennstaedtia punctilobula*	frond	1	18.59	447.36	24.06:1
Food diet in lab study	-	3	5.68 ± 0.59	291.72 ± 9.82	51.36:1

* - samples were only consumed on the laboratory collection site, and in the laboratory

and late winter samples were combined. The bark values presented in Table 1 can be used to estimate the sodium concentration of food items consumed from October to April, but no species distinctions can properly be made because of the small sample sizes, the large number of factors which determine nutrient concentration both between and within a species (Srivastava 1964, Day and Monk 1977), and the sampling scheme used (Auchmoody and Greweling 1979). The concentration of sodium in bark is generally higher than in herbaceous vegetation (Likens and Bormann 1970, Day and Monk 1977). However, even using bark data, porcupine food sodium levels on the field study site ($\bar{X}$ = 6.6 mequiv/kg dry weight, n = 12) approximate those judged to be deficient in other studies conducted on sodium balance of herbivores: Blair-West et al. in 1968 (range 0.91 to 1.65 mequiv/kg dry weight); Hebert and Cowan in 1971 ($\bar{X}$ = 1.8 mequiv/kg dry weight); Weeks and Kirkpatrick in 1976 (range 1.68 to 4.47 mequiv/kg dry weight) and 1978 (range 0.61 to 9.1 mequiv/kg dry weight); Smith *et al.* in 1978 (range 4.5 to 22.7 mequiv/kg dry weight). It must be mentioned that these studies judged an environment to be deficient in sodium based on research conducted with laboratory and domestic animals. Weeks and Kirkpatrick (1978) noted that the sodium needs of wild fox squirrels and woodchucks are obviously lower, and the retension efficiency under normal conditions is higher than those of the laboratory rat, because mean sodium levels of almost all their plant foods are at least five to ten times lower than the minimum requirement for rats. Therefore, it is questionable if these environments are deficient or merely low in sodium, especially since minimum requirements have not been established for wild species.

High potassium concentration and a high potassium-to-sodium ratio have often been considered more important to sodium balance in herbivores than actual food sodium concentration. Potassium concentration of tree bark is generally much lower than in herbaceous vegetation (Likens and Bormann 1970, Day and Monk 1977). Thus data obtained from this study on potassium concentration (range 33.2 to 114.3 mequiv/kg dry weight) and potassium-to-sodium ratio (4.9 : 1 to 20.2 : 1) of porcupine foods are lower than values from other studies, where potassium rnaged up to 680 mequiv/kg dry weight and the potassium-to-sodium ratio reached 60 : 1 to 295 : 1 (Weeks and Kirkpatrick 1976, 1978). Smith _et_ _al_. (1978) found levels of sodium, potassium, and the potassium-to-sodium ratio in snowshoe hare food to be almost identical to those obtained in this study.

Porcupines obtained from the laboratory site were consuming almost exclusively acorns. This food source, which did not occur on the field study site, is low in sodium and high in potassium, resulting in an extremely high potassium-to-sodium ratio (Table 1). Weeks and Kirkpatrick (1978) found similar values in acorns and used these data to explain a secondary peak in sodium appetite in fall observed in fox squirrels. However, they do not consider increased squirrel activity resulting from recently weaned animals, or the increased need for sodium in growth of juveniles, as alternate explanations of this fall peak.

It was noted in this study that porcupines collected from the laboratory site were extremely fat, much more so than the field-site specimens. Two animals autopsied a week after capture had extremely high levels of internal and subcutaneous fat, the latter being in excess of 2.5 cm thick on the lower back. In contrast, all field specimens had little or no internal fat, and backfat measurements never exceeded 0.6 cm in thickness. It appears that porcupines on the laboratory site tolerate potential ion imbalance to feed on the nutritionally superior acorns.

In addition to acorns it was noted that many porcupines actively sought and consumed fronds of hay-scented fern (Dennstaedtia punctilobula). This food item, while being high in potassium, is quite high in sodium, resulting in a favorable potassium-to-sodium ratio (Table 1). It is not known to what degree this food source supplemented sodium intake, since no measurements were made of food quantities consumed. Weeks and Kirkpatrick (1976) suggested that consumption of fungi, which are rich in sodium, supplemented intake of this ion in white-tailed deer. Peak consumption of fungi and animal matter in squirrels coincides with reproduction, lactation and peak sodium appetite (Bakko 1975, Weeks and Kirkpatrick 1978). Jordan et al. (1973) studying moose on Isle Royale, concluded that were it not for summer consumption of aquatic plants, which are 50 to 500 times higher in sodium than terrestrial foods, these animals could not maintain a yearly balance of this ion. Dodge (1967) observed that large quantities of aquatic plants were consumed by porcupines in summer, though no importance was attached to this behavior.

Data obtained from the autopsy of porcupines in the field study are summarized in Table 2. Each parameter will be discussed individually.

In response to natural winter conditions a significant decrease in sodium concentration of serum and corresponding increase in potassium concentration was noted in the porcupines (Table 2). This was somewhat

Table 2. Seasonal values of porcupine necropsy data.

		Fall		Late Winter	
Sample - Type	n	($\bar{x}$ ± SE)	n	($\bar{x}$ ± SE)	
Blood - Na^+ (mequiv/1)	15	132.4 ± 1.22	18	119.9 ± 3.74	**
- K^+ (mequiv/1)	15	11.65 ± 0.90	18	17.02 ± 6.69	**
- Hematocrit	6	49.7 ± 2.33	18	62.5 ± 1.50	**
Kidney - Relative Medullary Thickness	16	3.35 ± 0.07	19	3.63 ± 0.07	*
- % water content	16	76.89 ± 0.70	19	77.00 ± 0.83	ns
Urine - Osmolality (mOsmoles/kg)	6	636 ± 57.9	10	896 ± 23.3	**
- Na^+ (mequiv/1)	7	2.87 ± 0.96	9	2.62 ± 0.54	ns
- K^+ (mequiv/1)	7	116.2 ± 19.5	9	111.8 ± 15.6	ns
Feces - % water content	15	58.03 ± 1.47	18	48.99 ± 0.94	**
- Na^+ (mequiv/kg dry weight)	16	14.52 ± 1.84	17	8.02 ± 0.48	**
- K^+ (mequiv/kg dry weight)	16	234.7 ± 15.8	18	135.4 ± 7.27	**
- Na^+: K^+		1 : 16.16		1 : 16.88	
Skeletal muscle - % water content	16	79.69 ± 0.26	17	79.29 ± 0.14	ns
- Na^+ (mequiv/kg wet weight)	16	20.58 ± 1.14	19	19.18 ± 0.52	ns
- K^+ (mequiv/kg wet weight)	16	97.32 ± 0.83	19	96.69 ± 0.64	ns
Liver - % water content	16	69.86 ± 0.30	19	70.90 ± 0.19	ns
- Na^+ (mequiv/kg wet weight)	16	35.20 ± 1.28	19	33.89 ± 1.13	ns
- K^+ (mequiv/kg wet weight)	16	78.58 ± 1.27	19	79.08 ± 0.88	ns

* Judged significant at the 0.05 level by use of Student's *t* test
** Judged significant at the 0.01 level by use of Student's *t* test

surprising considering that most mammals regulate these levels to be within fixed physiological limits. Division into separate sex and age groups shows variable response to winter (Table 3). Only juveniles and pregnant females were found to have a significant decrease in sodium concentration and increase of potassium concentration of serum. Juveniles would require extra sodium for growth (though no increase in mean juvenile weight was noted), and should cold exposure be a factor, they would be most cold-stressed because of size. Pregnant females require sodium for the developing fetus, placental complex and amniotic fluid. Non-pregnant females and adult males would be least stressed.

The majority of laboratory studies on the effects of low salt intake and cold exposure on plasma electrolytes conclude that neither stress results in any modification of plasma sodium or potassium concentrations (Bass and Henchel 1956, Coghlan et al. 1960, Kem et al. 1975). Some researchers, however, have shown that a diet deficient in sodium can reduce the level of plasma sodium (Erdosova and Kraus 1976, Young et al. 1976). In response to cold exposure in rats, Hannon et al. (1958) found a slight but significant increase in the level of plasma sodium, but suggest that this was an artifact brought about by hemoconcentration. Baker and Sellers (1957), in contrast, found no change under similar conditions in the rat. Neff (1966) noted an immediate decline in plasma sodium and increase in potassium in cold-exposed chipmunks, reaching its lowest point on the fourth day of cold treatment. Though levels returned to those of control animals by the end of the first week of exposure, at the end of the thirty-day-study, sodium concentration in plasma again fell below levels of control animals.

Field observations of serum electrolyte concentrations are

Table 3. Seasonal values of serum sodium and potassium levels from field collected porcupines.

Classification - parameter		Fall n	Fall ($\bar{x}$ ± SE)	Late Winter n	Late Winter ($\bar{x}$ ± SE)	
Juvenile	Serum Na^+ (mequiv/1)#	3	128.2 ± 1.3	7	109.1 ± 6.0	*
	Serum K^+ (mequiv/1)	3	11.3 ± 1.0	7	20.0 ± 2.0	*
Pregnant Female	Serum Na^+ (mequiv/1)	6	133.2 ± 2.2	6	118.9 ± 3.5	**
	Serum K^+ (mequiv/1)	6	11.0 ± 1.5	6	19.8 ± 2.5	*
Non-Pregnant Female	Serum Na^+ (mequiv/1)			1	131.0	
	Serum K^+ (mequiv/1)			1	10.0	
Adult Male	Serum Na^+ (mequiv/1)#	6	133.7 ± 1.7	4	137.5 ± 4.5	ns
	Serum K^+ (mequiv/1)	6	12.4 ± 1.9	4	9.3 ± 0.5	ns

- Significance was computed with the Cochran and Cox (1957) approximation of Student's t test for unequal observations and unequal variance.
* - Judged significant at the 0.05 level by use of Student's t test.
** - Judged significant at the 0.01 level by use of Student's t test.

somewhat limited. Again, most studies conclude no modification in the blood electrolytes result from low sodium environments or seasonality (Bakko 1975, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976). Blair-West et al. (1968) found a depressed concentration of plasma sodium (139 mequiv/l) in kangaroos from a low sodium environment versus one containing adequate sodium (148 mequiv/l). Smith et al. (1978) working with snowshoe hare found similar data in evaluating blood electrolyte levels during periods of sodium stress (April through July) caused by increased potassium-to-sodium ratio and potassium concentration of food items versus winter values (January through March). With the exception of juvenile males, their data indicated that all age and sex groups had a lower sodium concentration in blood during periods of stress, though only in yearling males were the levels significant (144.3 mequiv/l in January to March versus 124.2 mequiv/l in April to July). Examination of their data indicates high levels of individual variation occurred, an observation likewise noted in porcupine measurements of this study.

Packed cell volume of the animals in the field was shown to increase significantly from the fall to the winter (Table 2). The magnitude of this increase cannot be compared with other studies because of use of a non-standardized centrifuge, though methods used indicated a rise did occur. Sealander (1964) and McLean and Lee (1973) both noted a seasonal peak in hematocrit occurring in winter. Withers et al. (1979) found that arctic mammals have a higher hematocrit in relation to comparable temperate-zone mammals or to the same species from lower latitudes. Hagsten and Perry (1975) noted an increase in packed cell volume of lambs in response to a low sodium diet.

Porcupine urine osmolality was found to increase in winter relative to samples collected in the fall, but no difference was noted in sodium or potassium concentrations (Table 2). Very few researchers have made field measurements of these parameters in salt-stressed herbivores. Blair-West et al. (1968) monitored sodium and potassium levels in urine collected from sodium-stressed rabbits throughout the year. They found seasonal variation in urine electrolytes with a winter peak of sodium concentration (6 mequiv/l) relative to spring, summer or fall (0.59, 0.53, and 2.6 mequiv/l respectively). No attempt was made to explain the seasonal variation in sodium concentration, but it was not correlated with potassium concentration, which was high in all seasons (range 209 to 466 mequiv/l). It is possible that seasonal change in food levels were responsible. Weeks and Kirkpatrick and Smith also noted low sodium and high potassium concentrations in field-collected urine during all seasons. White-tailed deer had urine sodium concentrations ranging from 0.4 to 7 mequiv/l, with potassium 160 to 230 mequiv/l (Weeks and Kirkpatrick 1976). Snowshoe hares were found to contain urine sodium concentration below one mequiv/l while potassium ranged from 23 to 305 mequiv/l (Smith et al. 1978).

In an unprecedented study by Bakko (1975), urine osmolality and potassium, sodium and urea concentrations in red and gray squirrels were monitored throughout the year. The peak sodium concentration of urine in red squirrels occurred in the January-February period (58.8 mequiv/l) with much lower levels in all other months (range 3.4 to 11.6 mequiv/l, means). Gray squirrels had elevated urine sodium from March through July (11.0 to 14.3 mequiv/l, means) in comparison to other portions of the year (3.4 to 8.7 mequiv/l, means). Bakko (1975) suggested that the variation seen could be explained by variation in food items, though he did not measure this parameter. Peak osmolality of urine in red squirrels occurred in November-December and in gray squirrels March-April, though osmolality remained high throughout the year, except for July in both species. Potassium and urea were found to be the major solute constituents. Both followed the same seasonal pattern as total urine concentration, but potassium was found to correlate much better with fluctuations in osmolality. Porcupine urine in the winter period had a higher osmolality than in fall, but no increase in potassium. Though urea was not measured, it is likely that this solute was responsible for the increase in osmolality noted.

It is apparent from the meager data available in the literature that many more field studies will be required to understand the influence of urine on salt and water balance in mammals. Laboratory studies may be invalid in this endeavor, because as soon as a wild animal is placed in the laboratory, it is subjected to an artificial environment and its responses in such a situation may well mask features that are important for success in the natural environment (Bellamy and Weir 1972, Bakko 1977).

Loss of sodium via the fecal route may well be more important to sodium balance in a mammal than sodium lost via the urine. Most laboratory studies on salt balance have neglected to monitor fecal loss of sodium (Grace _et_ _al_. 1979), though it has been shown that sodium levels in feces and urine normally decline during periods of sodium stress (Jones _et_ _al_. 1967). Though no change was noted in urine electrolyte concentrations, a decrease was observed in both sodium and potassium concentration of feces (Table 2). This observation, along with the modification in blood electrolytes, may indicate that some factor occurring between the fall and winter sampling periods created an increased need for sodium retention. No sex or age related differences were noted in the fecal electrolyte concentrations. The levels of ion constituents in winter (8.0 ± 0.48 mequiv Na/kg dry weight and 135.4 ± 7.27 mequiv K/kg dry weight) were very close to those occurring in hemlock needles (9.4 ± 1.5 mequiv Na/kg dry weight and 133.8 ± 12.4 mequiv K/kg dry weight), which made up the bulk of the winter food. However, fall fecal concentrations (14.52 ± 1.84 mequiv Na/kg dry weight and 234.7 ± 15.8 mequiv K/kg dry weight) were higher than all bark values collected during this period (range 3.58 - 12.41 mequiv Na/kg dry weight and 33 - 114.3 mequiv K/kg dry weight). But because of lack of snowfall, porcupine movements could not be documented, and other food sources may have been responsible for the discrepency of values. It is of interest to note that the ratio of the ions remains the same for each period. Smith et al. (1978) in a small sample of snowshoe hare feces, found both sodium and potassium levels to be below mean plant levels, though the exact food items consumed in the formation of the feces were not documented.

Fecal moisture has been shown to be very important in sodium loss via the fecal route. The spring shift to lush foods in herbivores results in a change in feces from hard dry pellets to soft amorphous masses or to diarrhoea (Jordan et al. 1973, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976) and has been shown to cause an increase in sodium loss and even sodium deficiency (Frens 1958, Hebert and Cowan 1971, Weeks and Kirkpatrick 1976). Porcupines in this study had well formed pellets in both seasons, but moisture content decreased in winter (Table 2). Skadhauge _et_ _al_. (1980) studied the effect of dehydration on the water content and electrolyte concentration in the feces of the dik-dik antelope. They found a reduction in fecal water content when the animals were dehydrated (56% to 45% water), but found no change in fecal sodium or potassium concentration. Porcupines were found to have a similar reduction in fecal water content, but had a significant decrease in sodium and potassium concentration, which indicates an increase in sodium and potassium retention. In terms of sodium retention and potassium excretion, it would be more favorable to excrete excess potassium via the urine.

The amount of sodium ultimately lost is dependent not only on the quantity of sodium per unit of urine and feces, but also the amount of each produced relative to food intake. Little is known of water turnover rates in free-ranging wild animals, but it is generally agreed that water flux is 2-3 times greater in summer than in winter (Longhurst _et_ _al_. 1970). Observations in the snow below station trees indicated that very little urine was produced, while large quantities of fecal pellets littered the ground. Since almost all water intake must come from the food source, it would appear that porcupines may be water stressed during prolonged stays in station trees during winter.

Modifications of the kidney RMT noted in this study may be in response to this water stress. Schmidt-Nielsen and O'dell (1961) found a close correlation between RMT and the ability to concentrate electrolytes in the urine. Changes in osmolality of urine and RMT (Table 2) observed in this study are consistent with this data. Comparison of mean values suggest age and sex differences. Juveniles were found to have an 8.6% increase in RMT, females a 9.4% increase, and males a 4.3% increase in winter. To my knowledge, no prior study has measured changes in relative medullary thickness in response to cold exposure in the laboratory or field. Bakko (1975) found that red squirrels inhabiting river bottoms had a significantly lower RMT value than those collected from upland coniferous and mixed hardwood habitats. Laboratory studies have shown that any condition or treatment which brings about a requirement for conservation of water results in an increase in RMT (Blount and Blount 1968).

Exposure of porcupines to natural winter conditions caused an increase in the size of the kidney (Figure 3). Relative to unit body length, the mean kidney weight increased from the fall to winter period by 36% in juveniles, 5% in adult and pregnant females, and 28% in adult males. Laboratory investigations of cold acclimation in mammals have shown an increase in kidney weight in response to cold to be a common phenomenon. In the pioneering work of Emery _et al_. (1940), female rats experienced a 12.7% increase in kidney weight and males an 18.5% increase. Neff (1966) noted a progressive increase in kidney weight in response to cold exposure in chipmunks, reaching 30% over control animals at the end of his 30-day study. Brown lemmings of both sexes experience a 10% increase in kidney weight in response to cold exposure, but in varying lemmings under the same conditions, females were seen to increase 30% and males only 17% (Berberich and Folk 1976). The impetus for increase in kidney size in response to cold exposure is unknown.

Measurements of the sodium and potassium concentrations and water content of skeletal muscle and liver showed no significant seasonal differences (Table 2). No difference was noted in liver weight,

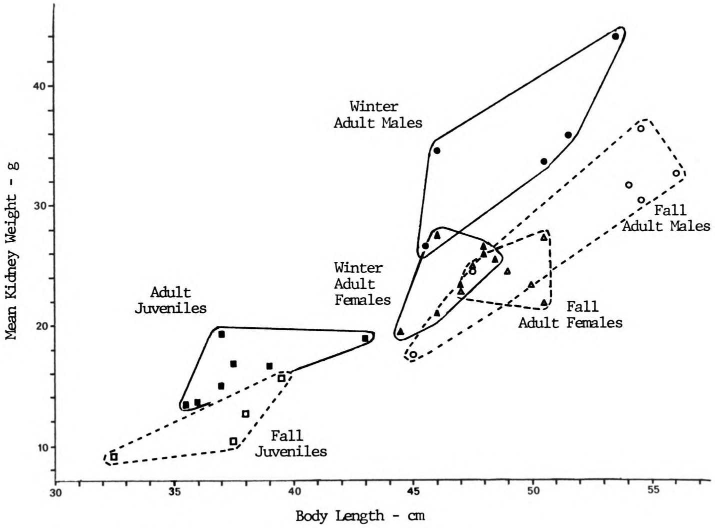

Figure 3. Porcupine mean kidney weight vs. body length.

though increase in liver weight has been noted in a number of studies of cold exposure in the laboratory (see Chaffee and Roberts 1971). Yunusov and Gitel'man (1974) reported severe modifications of sodium content in rat tissues when these animals were exposed to cold. They noted a decrease of 24 - 41% in sodium content of the majority of tissues (liver, kidney, thigh muscle, etc.) in comparison to a control group. No such modification was found to occur in porcupine tissues measured in this study.

The porcupine is unique among small North American mammals because of the length of the gestation period, which parallels that found in members of the Cervidae. Most females collected in November were found to be in the early stages of pregnancy, as evidenced by corpora lutea, swollen uteri and young embryos. By March, the developing young had grown to approximately one third of their birth weight of 400 to 600 grams (Shadle 1951). Only a single young is ever produced per female, but high fecundity is a rule. Fetus samples collected for analysis weighed 166, 192 and 194 grams. Moisture content averaged 80.5 ± 0.8 %, sodium concentration 78.8 ± 3.5 mequiv/kg wet weight and potassium 42.2 ± 0.4 mequiv/kg wet weight. The placental complex analyzed accompanied the 192-gram fetus and weighed 68 grams. Moisture content was 83%, sodium concentration 63.8 mequiv per kg wet weight and potassium 46.0 mequiv/kg wet weight. Four amniotic fluid samples showed a high degree of variability; the sodium and potassium concentrations in mequiv/l were: 76 and 6, 91 and 5, 80 and 6, and 134 and 10.5. No explanation is offered to qualify this high degree of variation though it may be an indication of the stress placed on females in reproduction.

Salt balance in porcupines may be complicated by their large parasite loads. Symons (1960) suggested that parasites inhabiting the intestinal system could jeopardize sodium balance. During casual observations in autopsy of field animals, it was noted that all animals were heavily parasitized with both Monoecocestus sp. and Wellcomia sp. Fecal pellets often contained visible proglottids and whole adult roundworms. Curtiss and Kozicky (1944) examined nine porcupines in Maine and found a mean count per animal of 766 tapeworms (range 124 - 1528) and 2524 roundworms (range 353 - 5184). Olsen and Tolman (1951) estimated one porcupine they autopsied to contain 30,500 Wellcomia.

Analysis of two tapeworm samples in this study found sodium concentration to be 345 and 377 mequiv/kg dry weight. If a porcupine in the field contained 200 grams of parasite, the total sodium tied up in this matter would approximate 3.6 mequiv. This would be roughly equivalent to the sodium contained in 380 g of hemlock foliage, about two days consumption if absorption were 100%. Since no study has documented the turnover rate of tapeworms or roundworms in porcupines, no estimate can be made of their importance in sodium balance.

Porcupines maintained in the outside holding enclosure used in the laboratory investigation appeared to be cold stressed. Piloerection was almost constant in all animals, and apparent shivering was noted on three occasions. The porcupines usually maintained the posture Clarke referred to as the ' lotus ' position, which is very effective at reducing heat loss through the poorly furred surfaces of the thorax and abdomen, and protects the bare foot pads (Clarke

1969a). Daily maximum and minimum temperatures recorded in the enclosure are presented in Figure 4. The mean temperature for the 24-day study period was - 6.8° C (range - 16° to 5° C). Records obtained from the National Climatic Center (National Oceanic and Atmospheric Administration, Ashville, North Carolina) indicate that no difference exists between the October through March temperature profiles of Lansing, Michigan and Ridgway, Pennsylvania. Clarke (1969b) recorded - 4° C to be the lower limit of the thermoneutral zone for porcupines collected in Massachusetts.

In contrast, animals maintained in the inside enclosure experienced little or no cold stress. After five weeks of captivity, one animal initiated a moult which continued until autopsy three weeks later. Only the wooly winter underfur was shed, no quills accompanied the balls of fur collected from the cage. A total of 52 grams of fur was collected, and the moult was not complete by autopsy. The stimulus for moulting could not have been day length, but light intensity and temperature may have been factors. No measurement was made of the sodium content of the fur, though this also may be relevant to salt balance. Franzman et al. (1975) found sodium in moose hair to vary seasonally with an average of 34.7 mequiv/kg dry weight.

Data from the laboratory study on salt balance are summarized in Table 4. Information obtained from individual animals is presented in order to illustrate the large variation observed between animals.

Porcupine food consumption compared favorably with that observed in a laboratory study by Bloom et al. (1973). They found daily consumption of Purina laboratory chow to be 135 - 150 grams daily for porcupines weighing 7.2 to 10.5 Kg. In this study,

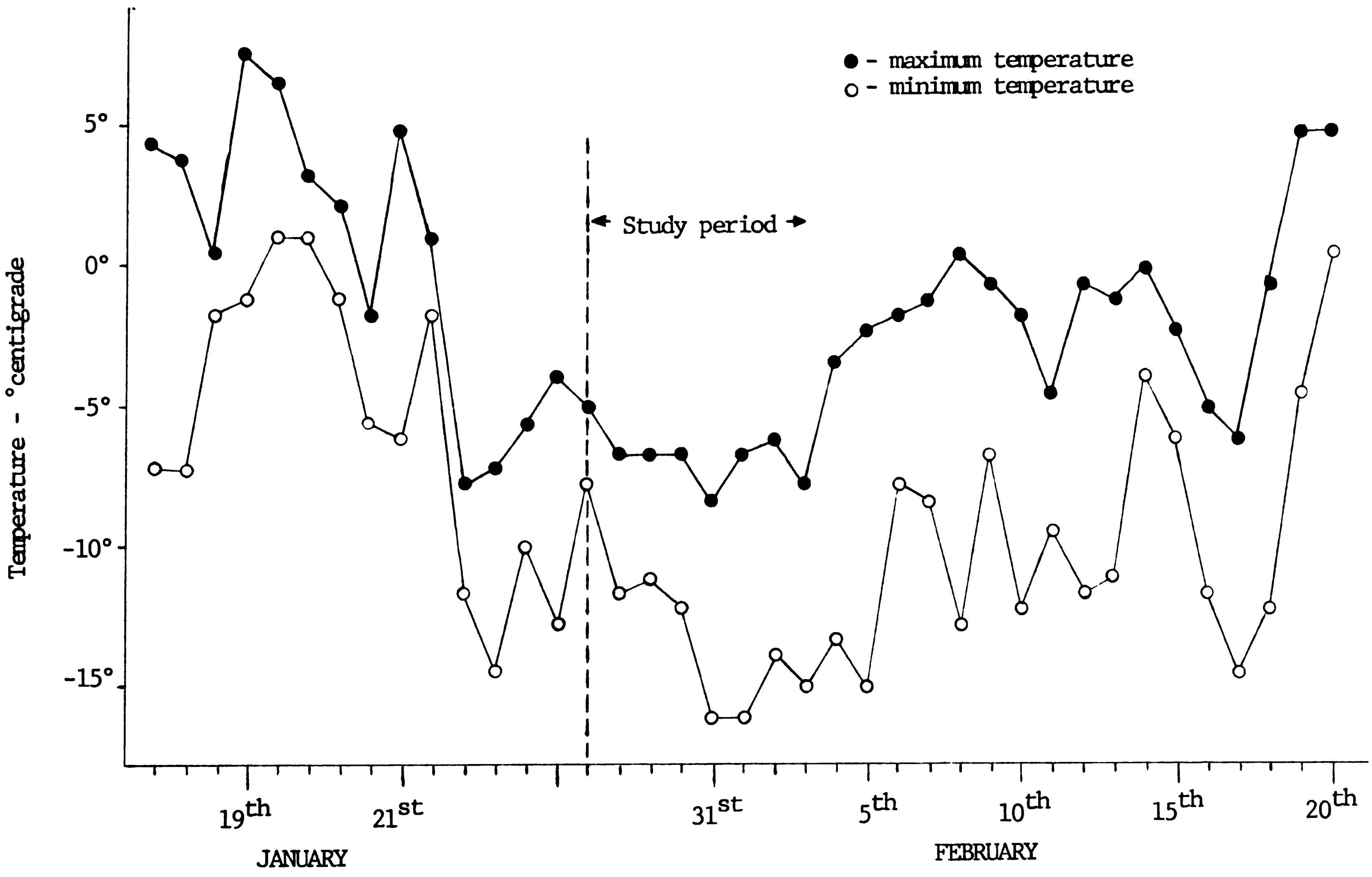

Figure 4. Daily maximum and minimum temperatures recorded from the outside holding enclosure.

Table 4. Summary of the laboratory study of sodium balance in captive porcupines held at room temperature and exposed to winter weather conditions.

Animal number	Classification Age - sex- condition	Maintenance condition I = inside 0 = outside	Weight (kg)	Mean Daily Food Consumption (g)	Mean Daily Feces Production (g) dry weight	Na conc feces (mequiv/kg dry wt.)	Mean daily urine Production (ml)	Na conc. urine (mequiv/l)	Total Na intake* (mequiv.)	Na loss urine* (mequiv.)	% loss in urine*	Na loss feces* (mequiv.)	% loss in feces*	Net Na balance* (mequiv.)
3	Juven. Male	I	3.3	89	19	6.65	74	1.50	11.11	1.99	40	2.98	60	+ 6.14
4	Preg. Female	I	4.4	48	13	36.3	52	1.77	6.00	1.44	32	5.12	78	- 0.57
7	Preg. Female	0	6.4	152	28	6.69	147	0.98	18.97	2.93	43	3.89	57	+12.15
8	Adult Male	0	5.3	188	37	7.66	184	2.95	23.49	10.43	64	5.88	36	+ 7.18
9	Adult Male	0	9.1	188	36	6.34	201	4.87	23.51	20.22	80	4.96	20	- 1.67
10	Juven. Female	0	3.4	92	17	5.49	76	1.12	11.53	1.94	48	2.10	52	+ 7.49
11	Adult Male	0	6.0	173	36	6.42	130	1.55	21.67	4.44	45	5.42	55	+11.81
12	Adult Male	0	4.8	129	24	6.49	130	1.30	16.15	4.09	52	3.73	48	+ 8.33

* - Data presented are from a 22-day period in which precise measurements were taken on sodium balance.

consumption ranged from 48 - 188 grams dry weight daily for 3.3 to 9.1 kg porcupines. Shapiro (1949) measured hemlock twig and foliar consumption to be 408 grams per day in a pregnant female (weight not given), but this figure represents wet weight and is only a rough approximation.

Measurements of urine production from this study do not agree with the work by Bloom _et_ _al_. (1973), who found urine production to be 347 to 371 ml per day. This discrepancy may be due to the difference in diet composition. Purina laboratory chow is 38 times higher in sodium than the diet provided in this study. The elevated water turnover rate observed by Bloom and his colleagues may have been in response to potential salt loading. Though they did not measure sodium concentration of urine, Fregly (1968) observed in rats fed a similar diet, a urinary sodium concentration averaging 160 mequiv/l. This illustrates a point. Because of the food diet used in most studies of salt balance, many comparisons with the state of animals in the wild are invalid.

Even with the limited sample size of this study, comparison of the data obtained on food consumption and feces and urine production shows definite trends with the maintenance conditions. Daily food consumption of the outside animals was greater, averaging 26.3 g food/kg body weight compared to 17.8 g food/kg body weight in the inside animals. This observation would be expected in light of the increased energy needs induced by cold exposure. The efficiency of food utilization in the outside animals was also greater; 19.2% of the dry food intake was excreted as dry feces in the outside animals versus 24.2% in the inside animals. Urine production per gram food intake was 0.93 ml in the outside animals, similar to 0.96 ml/gram food intake in the inside animals.

Sodium concentration of the feces was low in all animals except no. 4 (Table 4). Autopsy revealed that this porcupine was undergoing resorption of its fetus. Average sodium concentration of the feces in the remaining seven animals was 6.53 mequiv/kg dry weight, slightly above the food sodium concentration of 5.68 mequiv/kg dry weight. Urine sodium concentration was generally low in all animals ($\bar{X}$ = 2.01 mequiv/l), only slightly lower than in the field specimens. Six of the eight animals in this study were able to maintain a positive sodium balance in the presence of low sodium and high potassium levels in the food diet. Successful strategies included either low fecal sodium concentration or low urine concentration or both. Because of inadequate sample size, no comparisons can be made between the cold-exposed and room-temperature porcupines in these regards.

The limited autopsy data obtained from the laboratory animals are presented in Table 5. Hematocrit was high in all animals, though the higher values were recorded from the outside enclosure. Relative medullary thickness was relatively high in all animals, similar to values obtained from the March field collection. No increase in kidney weight was observed in either temperature condition, all weights being similar to the November field collection. The peak efficiency of sodium retention while consuming the laboratory diet was calculated to be 64 - 65% (Table 5).

Urine osmolality was measured only on January 25 samples. Urine was collected within an hour of excretion, sealed and stored frozen. Osmolality was higher in all outside animals (Table 5) than field

Table 5. Hematocrit, kidney RMT, urine osmolality and sodium retention abilities of captive porcupines.

No.	Classification	Maintenance Condition	Hematocrit	Kidney Relative Medullary Thickness	Urine Osmolality mOs/kg (Jan 25)	Net Sodium Balance	% Sodium Retension*
3	Juvenile Male	Inside	65	3.64		+ 6.14	55 %
4	Pregnant Female	Inside	63	3.63		- 0.57	
7	Pregnant Female	Outside	72.5	3.27	1659	+12.15	64 %
8	Adult Male	Outside	67	4.00	1124	+ 7.18	30 %
9	Adult Male	Outside	66	3.51	1144	- 1.67	
10	Juvenile Female	Outside	72	3.59	1395	+ 7.49	65 %
11	Adult Male	Outside		3.56	1784	+11.81	54 %
12	Adult Male	Outside	64	3.75	1466	+ 8.33	52 %

* - Refers to the amount of sodium extracted divided by the amount injested.

osmolality in either season (Table 2), though the composition of the food diet may have been a factor. Bakko (1977) noted a large disparity between urine collected from red squirrels shot in the field ($\bar{X}$ = 309 mOsmoles/l) and those trapped and held in captivity for 1 - 3 hrs ($\bar{X}$ = 2074 mOsmoles/l).

CONCLUSION

The spring peak in sodium appetite has been attributed to the increased water content, potassium concentration and potassium-to-sodium ratio of spring foods relative to those consumed in winter (Weeks and Kirkpatrick 1976, 1978). Although porcupine spring foods were not sampled in this study, earlier work by Leaf and Bicklehaupt (1975) in Armstrong forest can be used to estimate changes which occur in the spring shift from bark to foliage consumption. They measured sodium and potassium concentration of black cherry and sugar maple foliage for four summers. When comparing their data to those obtained in this study, all ion concentrations are seen to increase in the spring shift (winter black cherry bark - 7.3 mequiv Na/kg dry weight and 58 mequiv K/kg dry weight, summer black cherry foliage - 16 mequiv Na/kg dry weight and 289 mequiv K/kg dry weight, winter sugar maple bark - 5.36 mequiv Na/kg dry weight and 50.1 mequiv K/kg dry weight, summer sugar maple foliage - 8 mequiv Na/kg dry weight and 174 mequiv K/kg dry weight). The ratio of potassium to sodium also increases (black cherry bark 8:1 to 18:1 in foliage, sugar maple 9:1 in bark to 22:1 in foliage). Were this the extent of this study, conclusions similar to those of Weeks and Kirkpatrick (1976, 1978) may have been reached in order to explain the seasonal attraction to sodium. However, data obtained from the lab study indicate that porcupines are able to maintain sodium balance at levels of potassium as high as in the spring foliage (292 mequiv K/kg dry weight in the food diet) and at a higher potassium-to-sodium ratio (51 : 1). Work by Grace et al. (1979) showed that rabbits were able to adjust quickly to a change in the potassium-to-sodium ratio of 2 : 1 to 43 : 1, attaining near balance conditions in three days. In most if not all herbivores, increased potassium concentrations in spring foods do occur, but the influence this has on the sodium balance in the natural environment has not yet been substantiated.

The attraction and apparent craving of porcupines to items containing salt has been noted extensively. In the natural environment they often consume discarded antlers (239 mequiv Na/kg in white-tailed deer antlers, Weeks and Kirkpatrick 1976) or bones of dead cervids (130 ± 18 mequiv Na/kg in moose bones, Botkin et al. 1973). Porcupines are best known for their incessant gnawing of man-made objects and structures containing the attractant (Spencer 1950, 1962, Dodge 1967). The use of salt on winter roads may also effect this behavior. Brander (in Earle 1978) noted increased porcupine roadkills and activity along roadsides from mid April to mid June. This coincides with peak sodium appetite in porcupines (Campbell and LaVoie 1967) and may be related to the road licking behavior which Weeks and Kirkpatrick (1978) observed in this season in fox squirrels and woodchucks.

Some investigators have suggested that sodium appetite may simply be a common response of all mammals to the flavor of sodium and not be in response to sodium deficiency (see Denton 1967). This argument can be discounted in porcupines by the work of Bloom et al. (1973) who showed that when maintained on an adequate sodium diet, porcupines exhibited a negative preference for solutions containing NaCl. Furthermore, they found that porcupines could distinguish between deionized water and solutions at least as dilute as 0.5 mequiv. Na/l, which was the lowest level tested. The high degree of sodium attraction noted in porcupines is therefore probably in response to sodium deficiency coupled with their high responsitivity to sodium. To date, no researchers have attempted to qualify or quantify any specific plant feeding habit designed to obtain a higher intake level of sodium. Gill and Cordes (1972) suggested that fat content of food was very important in food species selection in the natural winter environment. Spencer (1950) noted a specific feeding pattern enabling porcupines to ingest bark containing higher levels of sugar. The microenvironmental changes among and within trees, as well as their individual status, would provide infinite variation in mineral content of vegetation (Day and Monk 1977, Auchmoody and Greweling 1979) and thus would complicate similar studies of this nature on sodium attractants.

Dehydration in response to cold may have a major influence on the seasonal salt appetite. Water content of skeletal muscle, liver, and kidney in this study was not modified by the cold winter conditions, though total body water content was not measured. Longhurst et al. (1970) found that thigh muscle moisture content of black-tailed deer also was not modified by winter, but found that the percent body weight as water changed significantly from 73.5% in summer to 63.4% in winter. This indicates extracellular dehydration. In the laboratory, dehydration in response to cold has been observed in a number of mammals, always accompanied by the loss of sodium required to maintain homeostasis of body fluid composition (Fregly 1968, Neff 1966, Ringens _et al_. 1977). This dehydration appears to be maintained in the cold (Box _et al_. 1973, Fregly _et al_. 1976).

Following extracellular dehydration, simple consumption of water which is low in sodium would be insufficient to rehydrate the body. When water is consumed, the body fluids become increasingly dilute, and water consumption must thus be stopped before fluid volume balance is restored. In this case, a sodium appetite is manifest, as the animal is attempting to restore not only the fluid but also the minerals within it, sodium being the major ion (Fitzsimmons 1975). If the total body water in a white-tailed deer decreased as much as that measured by Longhurst _et al_. (1970), the sodium necessary for replacement of isotonic body fluids in a 50-kg doe would be 12.3 grams, a considerable amount since only 19 grams is required for production of twin fawns in that species (Weeks and Kirkpatrick 1976). By using the data of Weeks and Kirkpatrick (1976) on deer food sodium levels for the period of March to May, and a rough estimate of daily food consumption of 2.0 kg/day, at 100% efficiency, approxiamtely 105 days would be required to rehydrate the body. Indeed, the difficulty of increasing the body water pool may actually create a greater stress on sodium balance than reproduction, since it may occur in a shorter time span. The statement by Weeks and Kirkpatrick (1976) that in April there are "no intrinsic, suddenly imposed stresses common to all ages and sexes" may be unfounded.

This study has demonstrated that no intracellular dehydration of tissues occurs in porcupines (Table 2). Unfortunately, extracellular dehydration was not investigated, though, because of their sedentary habits and ease of capture, porcupines would be excellent study animals for replication of work by Longhurst et al. (1970).

Fregly et al. (1976) suggested that cold-induced dehydration may be beneficial for survival in the cold, but offered no mechanism. Ringens et al. (1977) cited an obscure paper by Reader (1952) in suggesting that thermal conductivity of tissues decreased with decreasing water content.

The changes in the kidney noted in this study may be due to the probably water stress of porcupines, or primarily for reduction in water turnover rate. Longhurst et al. (1970) measured a decreased water turnover rate in winter deer, 1.75 l/day in 33 kg animals, compared to 3.33 l/day in 32 kg animals in summer. Reduction in water turnover rate would benefit thermal balance, while at the same time possibly reducing sodium loss via the urine because of reduced volume. The most available water source in winter is ice and snow. When one considers that this source must be melted and warmed to the temperature at which it is lost, a process which at - 10° C would require approximately 166 calories/g, the benefit of reduced water turnover rate is obvious.

The modification in hematrocrit noted in this study and others may also be in response to water stress combined with thermal stress. Fregly (1967) noted that evaporative water loss from rats is nearly doubled during exposure to cold. Withers et al. (1979) calculated that expired air is a significant avenue of heat loss and can comprise 10% or more of the metabolic heat production, even at low ambient temperatures. Blood with higher hematrocrit and hemoglobin content has a greater oxygen extraction ability and thus possibly can reduce both heat and water loss (Withers et al. 1979).

Thus the water, sodium and thermal balances of a mammal are intimately interrelated. It appears from this study and review of the literature that sodium appetite would be greatest in spring. However, in the porcupine there appears to be a sodium stress in winter which is not caused by increased water intake, attempts at rehydration or shifts in food diet which occurs at a later time. The cause of this stress can only be speculated upon.

Neff (1966) noted that mechanisms responsible for the active restoration of sodium and potassium to normal levels, following modification occurring after cold exposure, were triggered only after sufficient violation of ion homeostasis. His data suggested that the sudden alterations in metabolism resulting from acute cold exposure caused a temporary ion imbalance. This effect may be compounded by the continuous fluctuations of temperature in the natural winter environment. Throughout its range, the porcupine experiences temperatures far below the recorded thermoneutral zone (the minimum temperature on one field collection day in Pennsylvania was - 24° C), and a fluctuation of 30° C in a 24 hr period is not uncommon. In many areas, dens are not available, and occupation of station trees increases heat loss by wind and radiation. These conditions necessitate constant changes in metabolic rate, which may be the cause of the socium stress observed.

The shifts in metabolic heat production which may cause ion imbalance may be due to the use of the sodium pump, which appears to be a means of increasing cellular thermogenesis (Himms-Hagen 1976). No research has been attempted at monitoring sodium balance in a continuously fluctuating environment, and thus the relationship between cold exposure and sodium balance is unknown.

Observations of porcupines in their natural winter environment, coupled with data obtained from this study, provide an excellent opportunity to estimate late winter sodium and water balance. During this time, porcupines are almost exclusively consuming hemlock foliage and bark. They often remain for up to a month in this species as a station tree, during which almost all water must come from this food source. A small amount of water would be present in the form of snow, but much of the time this source is not available.

If we assume in late winter that a 5 kg porcupine consumes 200 g dry weight of hemlock foliage per day, a crude estimate can be made of the urine output and net sodium balance. The 200 grams of hemlock foliage (using Table 1) would contain 1.88 mequiv sodium and 26.76 mequiv potassium. If 20% of the dry food intake was excreted as dry weight feces, which data from the lab study indicate is a good approximation, using winter feces data (Table 2), the daily 40 gram feces output would contain 5.42 mequiv potassium, 0.32 mequiv sodium, and about 40 ml water. The remaining potassium, which would exit the body via the urine, would require 191 ml of urine and contain 0.50 mequiv sodium (Table 2). Net sodium gain, by these rough approximations, would be + 1.06 mequiv/day, for an efficiency of 56%. No estimate of the respiratory water loss in the porcupine exists, but at least 231 ml of water would be required daily for maintenance of this 5 kg porcupine.

A similar computation was made using a daily food intake of 200 grams dry weight of hemlock bark. From this calculation, only 11 ml of urine would be required to maintain equilibrium in potassium balance, and therefore approximately 51 ml of water would exit via feces and urine. The net sodium balance, while consuming 100% hemlock bark would be + 0.196 mequiv sodium per day for 36% efficiency.

These data can only attain relevance when combined with an estimate of the sodium required in reproduction and yearly growth. The average birth weight of a porcupette has been recorded to be approximately 500 grams (Shadle 1951). Data collected from 11 fall-winter juvenile porcupines in this study showed a mean weight of 2.65 kg, an increase of 2.15 kg over birth weight. Average fall-winter yearling weight of 5 animals was 4.75 kg, an increase of 2.1 kg over juvenile weight. Ten animals judged to be 2 1/2 years old were found to weigh 6.25 kg, an increase of 1.5 kg in body tissue. However, yearling females may become pregnant, and the sodium required in reproduction would be roughly equivalent to 0.6 mequiv. By these data, it appears that the first three years of growth and reproduction would require sodium for production of 2.1 kg of body tissues per year. Beyond this age growth slows down and sodium stress would decrease.

For mammals, sodium is a major constituent, comprising about 0.15% of live body weight. The value of 2.1 kg of body tissue would thus contain 137 mequiv of sodium. This quantity, if spread equally through the year, would necessitate a net requirement of + 0.375 mequiv/day. From the above calculations, it was shown that a porcupine consuming 200 grams dry weight of hemlock bark per day, would only obtain 0.196 mequiv sodium and thus could not maintain sodium balance through the year on this food source. Hemlock foliage, at

+ 1.06 mequiv/day, would provide the necessary sodium required for growth.

Analyzing the data obtained from the necropsy samples there appears to be a severe sodium stress imposed between the fall and late winter periods. This occurred in light of the diet composed primarily of hemlock foliage and the reduced growth rate in winter. Between the two sampling periods, some unknown factor must have acted upon the porcupines causing this sodium stress. By mid-winter the stress may have sufficiently threatened survival to a point where all efforts to retain sodium were maximized. This could explain the efficiency noted by late winter in this study, and the high death rate in wintering juveniles (Smith 1977).

At normal porcupine food consumption, many food sources would not contain adequate sodium to maintain a net balance with the environment. A porcupine consuming acorns with 64% efficiency in extracting sodium, would need to consume 600 grams dry weight of acorns per day, over three times normal consumption. Selective feeding, similar to that observed in moose by Jordan (1973) must definitely exist.

The potential for sodium stress in the porcupine is very real. It has been shown in this study that cold exposure can affect sodium balance in many ways. The outward manifestation of sodium deficiency in a mammal would most likely be reduced productivity and increased abortion. Shapiro (1949) suggested abortion was common in porcupines, though Dodge (1967) found little evidence of prenatal death (only two females of more than 200 autopsied had indications of resorption of the fetus). In this study, 10 adult field collected females in mid-term were examined and one of these was in the process of resorption. Because of high fecundity, in porcupines, net productivity could easily be examined by total coverage of an area and comparison of the number of juveniles to adult females. Because of these easily measured parameters, their food habits and long gestation period, the porcupine would present a convenient sized analogue to the large cervids. Though certain problems do exist, as they do in all research, further investigation into the various aspects of sodium balance in the porcupine may prove to be very enlightening.

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