1977

Biology of the Porcupine (Erethizon Dorsatum) in northwestern South Dakota

Judith Johnson

BTOLOGY OF THE PORCUPINE (<u>ERETHIZON DORSATUM</u>)

IN NORTHWESTERN SOUTH DAKOTA

by

Judith Johnson

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

BIOLOGY OF THE PORCUPINE (*ERETHIZON DORSATUM*) IN NORTHWESTERN SOUTH DAKOTA

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

ACKNOWLEDGMENTS

Appreciation is extended to my graduate advisor, Dr. Frank Shitoskey, Assistant Leader, South Dakota Cooperative Wildlife Research Unit, for his advice throughout the project and aid in thesis preparation and review.

Special thanks are extended to Kenneth Solomon for his patience and assistance with laboratory and field work. I also wish to thank technicians Wayne Winter and Brian Gueck for assistance in field work, and Sandy Amazeen for assistance in the lab. Thanks are also given to fellow graduate research assistants Norm Messenger, Maureen Beckstead, and Chuck Blair for their help and encouragement.

The assistance of Dr. Burruss McDaniel, Entomology-Zoology Department, and Elizabeth Sheldon, Department of Wildlife and Fisheries Sciences, South Dakota State University, in identifying parasites is appreciated.

Research was funded by the Office of Biological Services (U. S. Fish and Wildlife Service, Washington, D.C.) Contract No. 14-160008-1181 through the South Dakota Cooperative Wildlife Research Unit (U. S. Fish and Wildlife Service, South Dakota State University, South Dakota Department of Game, Fish and Parks, and the Wildlife Management Institute, cooperating).

JAJ

ABSTRACT

The summer home ranges, food habits, cover preferences, population dynamics, metabolic rates, growth rates, and taxonomic characteristics were determined for porcupines (*Erethizon dorsatum*) in northwestern South Dakota. The summer home ranges were 158.2 ha for adult females, 90.4 ha for juveniles, and 57.9 ha for adult males. The population was 34 percent adult males, 16 percent juvenile males, 34 percent adult females, and 15 percent juvenile females. The preferred daytime cover choice was silver buffaloberry (*Shepherdia argentea*), followed by snowberry (*Symphoricarpos occidentalis*), earth dens, forbs, and low brush. Shrubs were the most important item in the diet, then trees, forbs, and grasses. Buffaloberry was the most frequently eaten shrub, hawthorne (*Crataegus* spp.) was second. Ponderosa pine (*Pinus ponderosa*), willow (*Salix* spp.) and green ash (*Fraxinus pennsylvanicus*) were the most common tree species consumed. Alfalfa (*Medicago sativa*), wild licorice (*Glycyrrhiza lepidota*), yellow sweetclover (*Melilotus officinalis*) and bigtop dalea (*Dalea enneandra*) were the most frequently utilized forbs. Porcupine assimilation efficiency of pine inner bark was 83.6 percent; the assimilation efficiency of alfalfa was 77.6 percent. The resting metabolic rate of adult porcupines in thermoneutrality was 64.67 $W(kg)^{0.77}$ kcal/day. The upper critical temperature was 23 C. Rises in metabolic rate with ambient temperatures above 23 C followed the equation RMR = 15.24 + 1.15 X, where X is ambient temperature. Skull characteristics, external

measurements, and coloration indicated that the population in Harding County, S. D. is an intergrade between E. *dorsatum* *bruneri* Swenk and E. *dorsatum* *epixanthum* Brandt.

TABLE OF CONTENTS

LIST OF FIGURES

LIST OF TABLES

INTRODUCTION

The porcupine (*Erethizon dorsatum* Linnaeus) is traditionally considered detrimental to and dependent upon forests. Most studies of the species have concentrated on coniferous areas. However, a number of records in the literature describe the occurrence of the porcupine in such diverse vegetation types as oak woodland, riparian, mesquite, creosote bush, and oak pine (Chew 1960), desert shrub (Reynolds 1957), and prairie (Taylor 1935).

There are seven subspecies of New World porcupines (Hall and Kelson 1959). The porcupine found in western portions of the Dakotas, eastern Montana, Wyoming and Colorado, northwestern Oklahoma and Texas, Kansas, and Nebraska is *Erethizon dorsatum bruneri* Swenk (Nebraska yellow-haired porcupine). It intergrades to the north and east with E. *dorsatum dorsatum* Linnaeus and to the west with E. *dorsatum epixanthum* Brandt (Hall and Kelson 1959).

The objectives of this study of the porcupine in the prairie of South Dakota were: (1) to determine the home range, seasonal migration patterns, and cover preferences; (2) to determine food habits and assimilation efficiencies of major components of the diet; (3) to determine population dynamics, including age ratios, reproduction rate, and mortality factors; (4) to determine energy requirements and response to cold and heat stress; (5) to investigate physical and behavioral development of the young; and (6) to add to the taxonomic knowledge of the subspecies.

STUDY AREA

Field studies were conducted in Harding County, S. D. (Fig. 1). Most of the area is a treeless, semi-arid rolling prairie with isolated plateaus and buttes. The average elevation is approximately 1000 meters. The climate is severe, with short hot summers, long cold winters, and rapid fluctuations in temperature. The average annual temperature is 9 C; the January mean is -9 C and the July mean is 22 C. The frost-free season lasts from late May to mid-September (Spuhler et al. 1971). Most of the 34 cm annual precipitation falls as short, hard thundershowers in spring and early summer. Snowfall averages 13 cm and is often accompanied by strong winds.

Most of Harding County is in the Grand River drainage. The Little Missouri River drains the northwestern portion of the county while the southern portion is in the Moreau River drainage. Most small streams are intermittent. Except for intervals after rains, there is little standing water on the prairie.

The native vegetation of Harding County is a shortgrass prairie association of wheatgrass (*Agropyron* sp.), blue gramma (*Bouteloua gracilis*), and little bluestem (*Andropogon scoparius*) (Westin et al. 1967). Approximately 88 percent of the county is in rangeland, 10 percent in croplands (primarily wheat), and 2 percent in woodlands (Spuhler et al. 1971). There are three small areas of forest: the Cave Hills in the north central portion, the Slim Buttes in the east, and the Short Pine Hills in the southwest. Ponderosa pine (*Pinus ponderosa*) is distributed along the edges of the buttes, which have

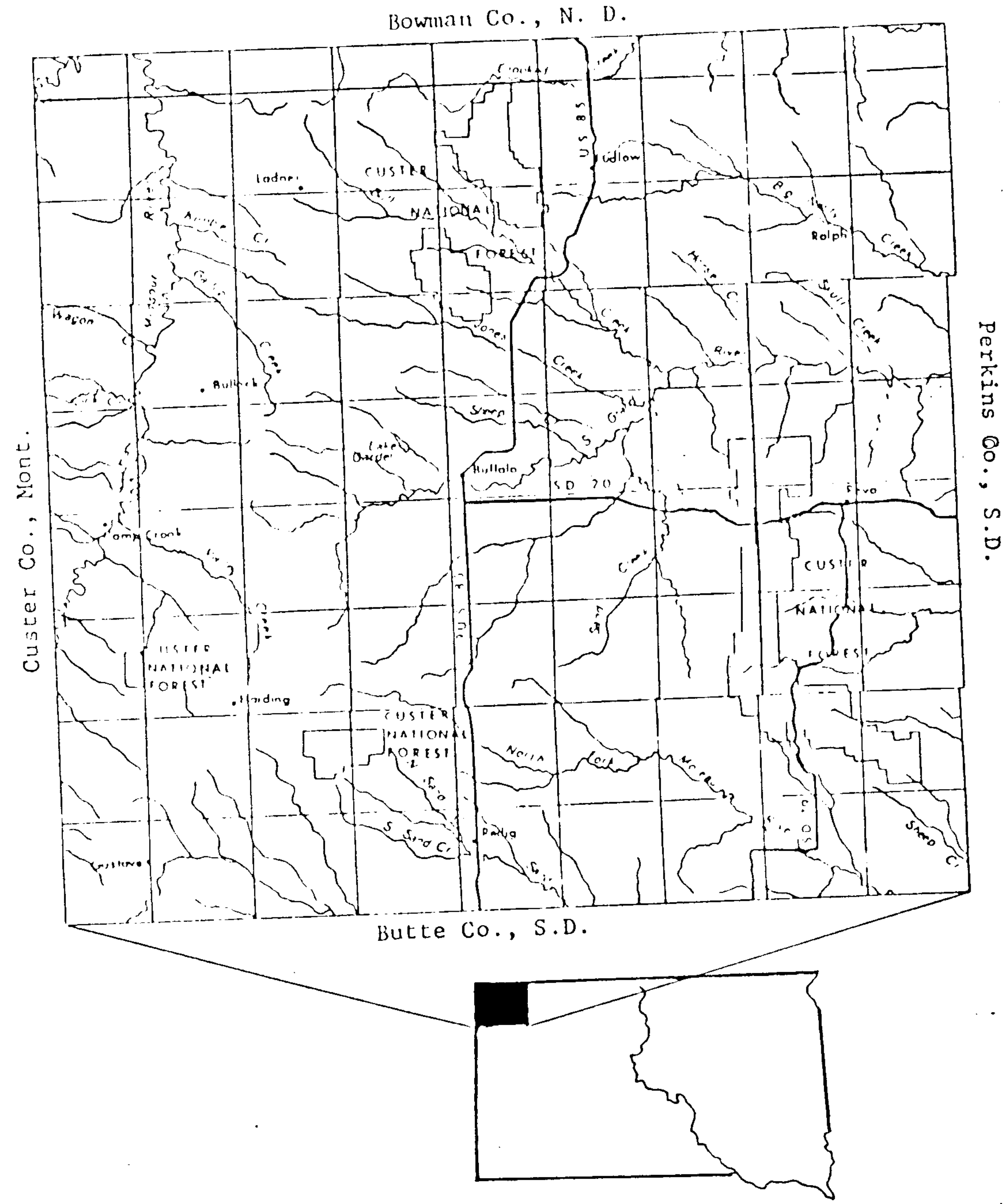


Figure 1. Harding County, South Dakota.

open grasslands on top. There are shallow rock walls 3 to 15 m high and associated small talus slopes around some edges of the buttes. Badlands, areas with steep slopes and little or no vegetation, are scattered throughout the county.

Ash (*Fraxinus pennsylvanicus*), elm (*Ulmus* spp.), and willows (*Salix* spp.) grow in the draws leading down from the buttes and along the larger waterways of the prairie. Boxelder (*Acer negundo*), cottonwood (*Populus deltoides*), and poplars (*Populus* spp.) are also common. Willow, cottonwood, and populars have been planted along some creeks and farm ponds. Aspen (*Populus tremuloides*) is locally abundant on slopes of larger forested buttes.

The more common brush species surrounding local buttes and creeks are buffaloberry (*Shepherdia argentea*), snowberry or buckbrush (*Symporicarpos occidentalis*), hawthorne (*Crataegus* spp.), currant and gooseberry (*Ribes* spp.), and wild rose (*Rosa* spp.). Buffaloberry and snowberry are also common on the prairie.

METHODS AND MATERIALS

Collection and Autopsy

A small area which included most of the major vegetation types and topographical features common in Harding County was chosen for intensive study by telemetry and capture-tag-recapture. The survey route through this area began in the prairie on S. D. State Highway 20 1 km west of the western boundary of Custer National Forest, crossed through the badlands and a small section of pine at

Reva Gap, then through prairie to S. D. State Highway 79, and 1.5 km south on 79. A second small section bisecting the South Slim Buttes on Highway 79 was used for tagging and collecting.

The roads through the intensive study area were surveyed from a vehicle by two people two or three nights per week from May to August, 1976, and one night per week from September 1976 to April 1977. The vehicle was equipped with a roof rack of lights which lit both shoulders of the road to 25 m from the road. A hand-held 250,000 cp spotlight was used as a supplement. The 14.5 km (nine-mile) route was driven from 2200 to 0200 hours, once in each direction. Areas away from the road were searched periodically on foot and horseback. Most porcupines seen between May and September 1976 were captured in a 38 l metal pail, etherized, weighed, measured (total, tail, hind foot, and ear lengths), sexed, examined for general condition and external parasites, tagged with plastic strips in both ears, and released. Recaptures were identified, weighed, checked for general condition, and released. Locations were marked on a 15-minute U.S.G.S. map. All animals found from October 1976 to April 1977 were collected for autopsy.

During autopsy animals were weighed, measured (total, tail, hind foot, and ear lengths), and examined for external parasites and general condition. The digestive tract, reproductive tract, and skull were removed. All other organs were examined for gross abnormalities in structure, location, or coloration. External parasites were identified by Dr. B. McDaniel (Entomology-Zoology Department, South

Dakota State University). Skulls were measured with dial calipers. Measurements taken were:

1. Width of mandible outside condyloid processes.

2. Length of right mandible from posterior point of condyloid process to posterior of incisor alveolus.

3. Length of mandible from anterior incisor alveolus to posterior margin of angular process of right mandibular ramus.

4. Mandibular height from base of angular process of right mandibular ramus to top of right condyloid process.

5. Skull length from anterior edge of right premaxilla to posterior edge of right occipital condyle.

6. Zygomatic breadth (widest diameter of skull, at outer surface of zygomatic arches).

7. Mastoid breadth, between outer posterior margins of the mastoid processes.

8. Least interorbital width.

9. Diastema, from posterior edge of right incisor alveolus to anterior edge of right premolar alveolus.

10. Molar axis (length of tooth row from anterior edge of right premolar alveolus to posterior edge of alveolus of right third molar).

11. Greatest length of right nasal bone.

12. Anterior width of nasal bones.

13. Posterior width of nasal bones.

14. Weight of skull.

Width of mandible (1) and length of mandible (2) were used in addition to tooth wear and replacement (Dodge 1967) to divide the skulls into seven age-groups. Statistical analysis of external measurements was by one-way analysis of variance by sex. Duncan's test was used between means. The least-squares method was used to analyze skull measurements between ages and sexes (Steel and Torrie 1960).

Food Habits

The year was divided into 6 sample periods of 2 months each for analysis of food habits. Available vegetative types, snow cover, and porcupine activity levels were similar in each of the 2-month periods. Van Bruggen (1976) was used for scientific names of plants. Stomach and terminal 1 m of intestine contents were treated as two separate food-habits collections. One hundred and twelve collections were examined from 78 individuals. Frequency and density of species and vegetation types were calculated from fecal samples only, to eliminate duplication from individual preference. All stomach and fecal samples collected from autopsies and telemetry animals were washed, dried to constant weight, and ground in a Wiley mill to pass through a 1.0 mm screen. Five microslides of each sample were made, each having a density of 3 plant fragments per 100x field. A total of 100 fields was read from each sample, 20 per slide (Hanson 1971). Only those fragments recognized as epidermal tissue were recorded as evidence of presence of a plant species at a location on a slide. A type slide collection was made of common species of plants from Harding County to facilitate identification. Also, a black-and-white photomicrographic atlas of identifying characteristics of each species was made for quick reference. Fragments were recorded as grass, forb, shrub, or tree.

The number of locations where a vegetative type occurred out of 100 locations was expressed as percent frequency of each vegetative type. The frequency was converted to density of particles per location using a table developed by Fracker and Brischle (1944). The density of particles per location was converted to percent relative density (RD) by the formula:

$$RD = \frac{\text{Density of particles of vegetative type A}}{\text{Density of particles of all vegetative types}} \times 100 \quad (1)$$

The percent relative density and actual percent dry weight were the same for grasses, forbs, and grass-forb combinations (Hanson 1971). It was assumed for purposes of analysis that the same principle holds true for shrub and tree fragments and combinations of all four vegetative types.

The digestibility and assimilation efficiency of alfalfa (*Medicago sativa*) and ponderosa pine were determined in feeding trials. Adult porcupines were confined to pens approximately 1 m^2 with floors of 2.5 cm x 5.0 cm wire mesh. A second floor of 0.6 cm^2 mesh was placed 5.0 cm below the first to catch feces and plant fragments. Animals were acclimatized to feeding trial procedures and diet for 3 days and then fasted for 24 hours prior to each 4 to 8 day trial. The feeding trial rations consisted of freshly cut pre- and early-bloom alfalfa and ponderosa pine saplings (5 to 9 cm diameter) and branches (2 to 5 cm diameter) cut into 0.3 m lengths with all needles removed prior to weighing and feeding. A control ration was used to determine overnight weight loss of forage. The inner bark from the pine control, fecal samples, alfalfa controls, and unconsumed forage were dried to constant weight in a 60 C oven before weighing. The porcupines were weighed at the end of both the acclimatization and feeding trials. Seven animals completed trials on alfalfa and six animals completed trials on pine.

Composite samples of feces and forage controls were sent to Iowa Testing Laboratories Inc. (Eagle Grove, Iowa), for proximate analysis by techniques described by Horwitz (1975). All proximate values were calculated on a dry-weight basis. Assimilation efficiencies were calculated by the equation:

$$AE = \frac{I - F}{F} \times 100 \quad (2)$$

where I is the ash-free weight of food ingested and F is the ash-free weight of the feces (Soholt 1973). Digestion coefficients for protein, fiber, and nitrogen-free extract (NFE) were calculated by the equation:

$$DC = C - F \times 100 \quad (3)$$

where C is grams of a nutrient consumed, and F is grams of the nutrient excreted (Kamstra 1975). The digestion coefficient of fat was assumed to be 1; this value was multiplied by 2.25 because of the high energy value of fat (personal communication, L. Kamstra). Total digestible nutrients (TDN) was calculated for alfalfa, by the formula:

$$TDN = (\%\ protein)(DC) + (\%\ NFE)(DC) + (\%\ fiber)(DC) = (\%\ fat)(1)(2.25) \quad (4)$$

(Kamstra 1975).

Telemetry

Tracking studies were conducted between March and November 1976. Two sizes of transmitter and harness were designed; those for juveniles weighed 100 grams; those for adults weighed 150 grams. Adult transmitters had greater transmitting ranges and heavier harnesses. The radios transmitted a pulse on one of 12 channels (105.995 to 151.160 MHz) 0.15 MHz apart. A replaceable lithium battery pack powered each unit. A 12-channel receiver and 5-element directional antenna were used for tracking.

Newly-instrumented animals were caught three days after release for examination for abrasions and harness adjustment. Adults were not disturoed again, as disturbance apparently resulted in an unusually long movement the following night. Harnesses on juveniles were checked weekly and enlarged if necessary. Disturbance did not appear to affect juvenile movements. Porcupines were found between 1200 and 1700 hours, at least three times a week. Distance and direction from the last location and exact location by compass bearings on 2 landmarks were determined. Activity and cover were noted, along with surrounding vegetation height and species. Scats were collected if present.

To calculate the minimum home range of an individual, a line was drawn connecting the outside points of location and the area of the resultant polygon calculated (Mohr 1947). This method gave an accurate representation of home range size; the area within the polygon had uniform vegetative and topical features and would receive equal usage by the porcupine. I considered the home range delimited when its size no longer increased with additional locations.

Laboratory Colony Maintenance

A colony of 10 to 12 porcupines captured in Harding County was kept at the South Dakota State University Wildlife Lab for use in metabolic and digestibility studies. They were fed a ration of commercial rabbit chow, dried field corn, and dry dog food. Diets were occasionally supplemented with alfalfa hay, fresh alfalfa, vegetables, fruit, and pine branches. Salt was supplied in block form. A sulfa-based compound was mixed in the ration to treat enteritis. One or two animals were kept in each 10 m^2 outdoor cage. Juveniles were kept with their mothers until early fall. Animals that died were autopsied by the South Dakota Veterinary Diagnostic Laboratory, where bacterial, viral, and histologic tests were made to determine cause of death.

Energetics

Oxygen consumption of an adult male, barren and lactating females, and a juvenile was measured to determine resting metabolic rate (RMR). Animals were tested at 15, 20, 25, 30, and 35 C while in summer pelage. Four porcupines which had partially shed their winter coats were tested at 0 C. An airtight 38 1 aquarium with a plexiglass lid was used as a metabolic chamber. An intake valve and telethermometer were mounted in the lid; the outflow to a paramagnetic oxygen analyzer was a valve at the bottom of the chamber. Air flow rate was determined by oxygen consumption of the individual; flow was regulated so that oxygen did not fall below 18.5 percent, and varied between 3000 and 4500 ml/min. Air was drawn through the chamber, then through drierite tubes and flow meters to the oxygen analyzer. The chamber was placed in an environmental chamber, where temperature was controlled to within 1.0 C. Porcupines were acclimated for at least 1 hour to the chamber temperature before measurements were taken, then 6 readings taken 5 minutes apart were averaged. Outputs from the oxygen analyzer and chamber thermometer were recorded continuously on a chart recorder. Rectal temperature was taken before the animal was placed into the chamber and immediately after removal. Oxygen consumption was calculated only from non-post-absorbtive, quiescent animals. Values were corrected to standard temperature (273 K) and pressure (760 mm), to liters of oxygen consumed per 24 hours; this was multiplied by 4.7 kcal/l (Kleiber 1961) to obtain energy values.

Variations in deep body temperature over a 24-hour period were measured in three adult females. A thermal transmitter 9 x 15 mm was surgically implanted in the peritoneal cavity. The porcupines were placed in a 24 x 60 cm cage inside an environmental chamber where they were exposed to a light cycle of 12 hours daylight and 12 hours darkness. They were provided with food and water and were not disturbed for the duration of the test. The receiver was turned on for 1 minute each hour by a time clock, and the body temperature was recorded on a chart recorder. Each animal was tested for 3

RESULTS AND DISCUSSION

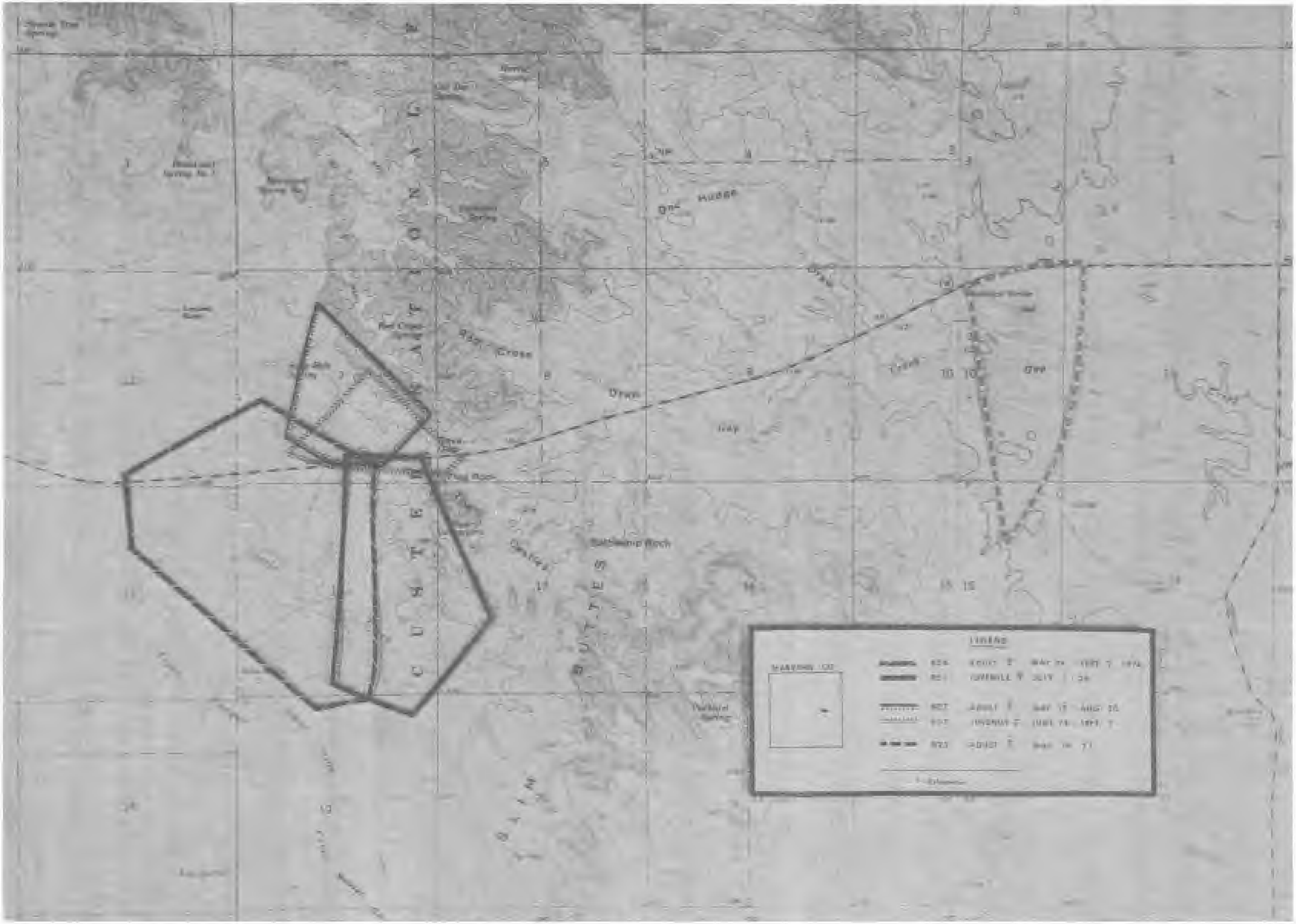
Home Range and Daily Movements

A total of 213 locations on 6 adult females, 3 adult males, and 9 juveniles were recorded. Home ranges were determined on 3 adult males, 2 adult females, and their 2 juveniles. The movements of 2 additional females were followed a sufficient number of times to determine cover preferences and daily movements, but not enough to determine home range. Nine other individuals were tracked for 2 to 3 days each to determine cover preference.

Home range maps of 3 adult females and 2 of their juveniles are shown in Fig. 2. The home ranges of the adult females were 303.4, 61.5, and 109.7 ha. The small home range (61.5 ha) was in a rugged badlands area, whereas the others were in more open, rolling country. The estimate of home range size of animal No. 823 (109.7 ha) was below the true range size since only 8 locations were taken, but probably delineates the north-south borders of her range.

Adult females tended to use their ranges differently than males or juveniles. Before their juveniles became relatively independent (at approximately 1500 grams), most of the adult females were located within an area of 1 ha or less, although this area did not necessarily include the juvenile. Animal No. 811 stayed near, although out of sight of, her newborn for 3 days following parturition; she then moved

Figure 2. Home range maps of adult female and juvenile porcupines.



C U S T E R   N A T I O N A L   F
B U T T E S
LEGEND
ADULT
JUVENILE
ADULT
ADULT

to a den 400 m away, leaving her young where it was born. Another female frequented rocky slopes 350-450 m from where her juvenile was found. When the juveniles were able to travel small distances and were on a solid diet, although not weaned entirely, the adult females began leapfrogging from one side of their range to the other, sometimes crossing over 1 km of grassland per night.

The range of one female could not be determined despite numerous daytime telemetry locations. She was instrumented in March 1976 and was located periodically until January 1977. From April 1976 tG January 1977 she occupied the same dirt den continuously, resulting in a calculated range and daily movement of 0 ha. However, her unweaned young was kept 400 m away from her den during the summer, and her December and March fecal samples showed that pine, the nearest of which grew 3-4 km away, was included in her diet.

The range sizes of juveniles reflected the size of the range of their mother. The ranges were 130.9 ha (mother, 303.4 ha) and 49.9 ha (mother 61.5 ha) (Fig. 2). The ranges of the juveniles overlapped but were not included entirely in the parental home range, except when the juveniles were very young. Juveniles generally began moving and feeding before dark, often in late afternoon, whereas adults did not become active until late in the evening, 2000-2200 hours. Marshall et al. (1962) observed that young porcupines tended to be more active in daylight hours than adults. The pairs he observed were rarely separated by great distances (average separation was 26.2 m) and moved together to new daytime resting areas. In Harding County the mother often traveled up to 0.5 km from her resting place to the unweaned juvenile.

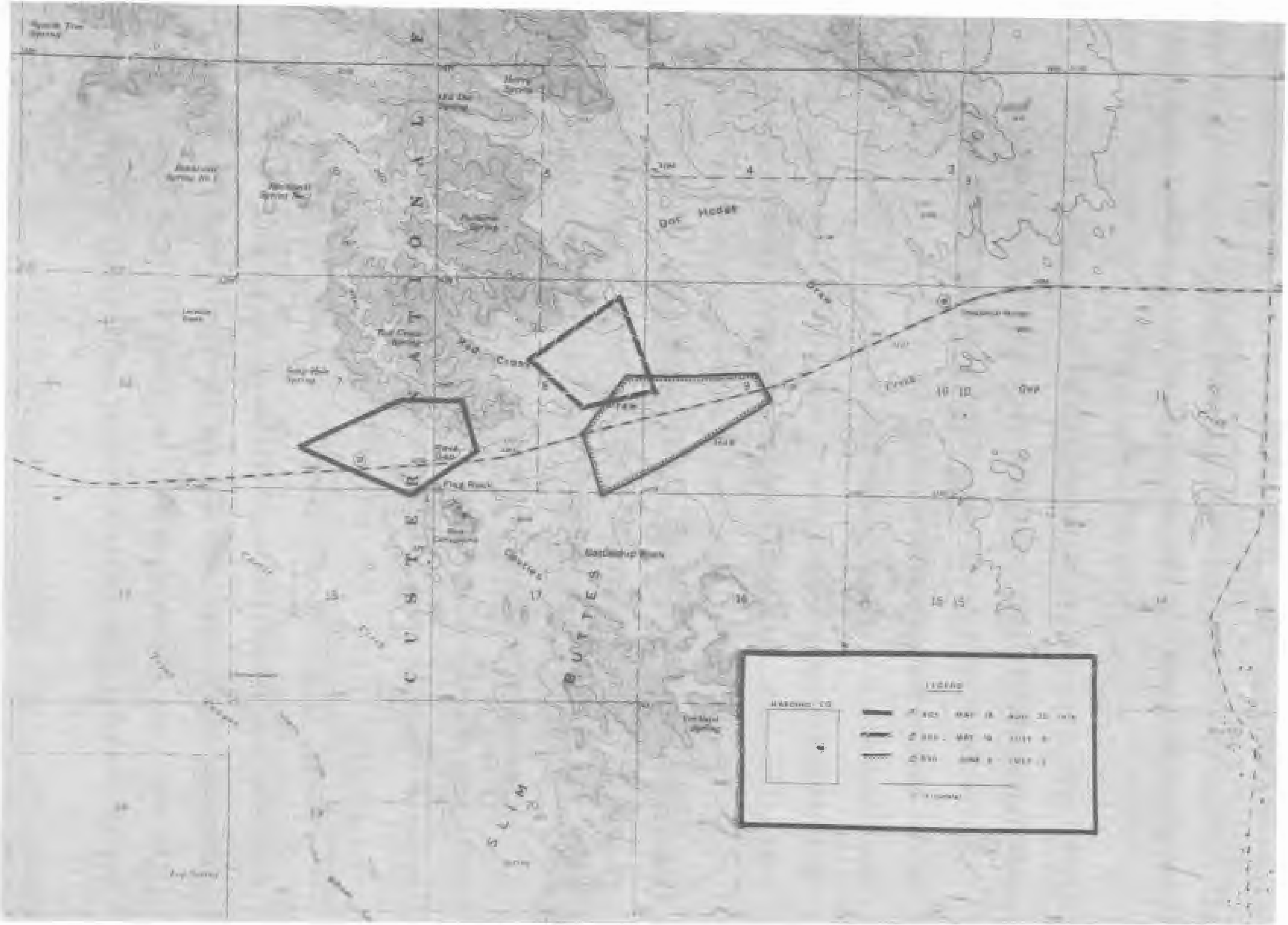
Adult males had smaller ranges during the summer months than either adult females or juveniles. Range sizes were 49.8, 53.4, and 70.4 ha (Fig. 3). Males were often found within a few meters of previous locations for several days to 2 weeks. They would suddenly make long movements to new areas where they would repeat the sedentary pattern.

Summer home ranges of all individuals were considerably larger than the 5.4 ha ranges described by Krefting et al. (1962) or the 17.3 ha range reported by Kelley (1970). Smith (1975) reported 22.6 to 82.0 ha home ranges for Washington porcupines.

Winter ranges were not determined by telemetry. Deep snows are rare and short-lived in Harding County, thus snow would not limit winter travel. Strong winds and extreme cold on the prairie may have restricted winter movements to sheltered draws or heavy brush. Some indication of winter ranged could be deduced from analysis of diet. Two animals were found living in permanent prairie dens 2.0 and 5.0 km from the nearest pines during winter. Fecal analysis showed both animals had been feeding on small amounts of pine. Occasional long winter movements are made, although animals may spend a day or two in transit, utilizing temporary dens.

Generally the distances moved per day in summer were 0-500 m for juveniles, depending on age, and 300-700 m for adult females. Long movements in summer were occasionally made; the maximum was

Figure 3. Home range maps of adult male porcupines.


Flag Rock
Battleship Rock
BUTTES
SLIM

1.6 km (straight line distance) over rolling prairie between 1100 and 2345 hours, for a nursing female. Her young was never positively identified, but 2 juveniles, both too young to travel, were found within 50 m of each other in the center of her range.

Newborn porcupines were unable to walk well for the first 3 days of life. When ; to 11 days old, (weighing approximately 1000 g) they began to move 3 to 5 m a night. By about 4 to 5 weeks of age (1500 g) they moved 50 to 75 m per night.

Attempts to determine ranges or daily movements from capture-recapture data were unsuccessful, since porcupine locations along roadsides seemed to be determined by topography. The porcupines traveled primarily down draws where more succulent vegetation or thicker cover could be found; thus animals were encountered on the road mainly at or near road-draw intersections. Although ranges of instrumented individuals extended as much as 2 km from roads, these porcupines were invariably captured during the night on a road close to the site of previous captures.

Home range size in mammals may be a function of metabolism and diet (McNab 1963). McNab developed two formulas for calculating home range size, one for croppers (grazers and browsers):

$$R_c \text{ (acres)} = .05 \text{ (70Wkg0.75)} \quad (5)$$

and one for hunters (carnivores, insectivores, and granivores):

$$R_h \text{ (acres)} = .20 \text{ (70Wkg0.75)} \quad (6)$$

In summer porcupines were croppers, feeding on common forbs and shrubs (Table 2); in winter they were hunters, traveling to scattered trees and shrubs, and probably shifting range size to R_h. Assuming food to be the major determinant of range size, the expected mean home range size for males would be 19.43 acres (summer) and 77.74 acres (winter); for females it would be 14.36 acres (summer) and 57.45 acres (winter). However, the actual home range size measured in summer was 5.87 ha (142.9 acres) for males and 158.2 ha (390.7 acres) for females. Metabolic requirements in summer must have a greater effect on porcupine movements than diet does, through either adverse environmental conditions or seasonal demands.

The magnitude of difference between predicted and actual values indicates high energy demands on porcupines, particularly on females and juveniles. Once juveniles are weaned, females do not need to travel to them each day and do not have the demands of lactation. All females showed large increases in weight through late summer and early fall, and retained high levels of body fat well into winter. Males, with summer home ranges 37 percent the size of nursing females, did not have to cope with demands of reproduction during that season. However, all males showed large weight increases through the summer, possibly in preparation for breeding season in fall. Males autopsied in late winter had low body fat levels.

I detected some seasonal movement, as has been reported in other areas (Taylor 1935). During summer, porcupines were abundant in prairie areas near the forested, rocky buttes surrounding Reva Gap, but few signs of porcupines were noted there during December and January. Fresh feeding activity in some areas of the buttes indicated a heavy population, suggesting that porcupines from the nearby prairie had moved up into the pines for the winter. Structures providing good winter cover for porcupines were scarce in the prairie; remaining animals lived in dirt dens, undercut banks, creek washouts, road culverts, dense thickets and haystacks.

Cover Preference

The habitat most often frequented by porcupines was silver buffaloberry, which composed 15.0 percent of all daytime telemetry locations (Table 1). Mixed brush (11.4 percent of locations) was also commonly utilized. The predominant species in mixed brush was buffaloberry, a thick, thorny, and nearly impenetrable shrub which offers good protection from terrestrial and avian predators as well as bad weather. Buffaloberry, as with pine in other areas, also serves as a year-round food source (Table 5).

Snowberry, representing 13.5 percent of all locations, offered no protection other than visual concealment. Because the shrub is deciduous, it would be of value only during summer months. It was not used as a food source. Snowberry forms patches a few meters across and provides heavier cover than surrounding prairie grasses and forbs.

Earth dens, composing 11 percent of the telemetry locations, were used by only 2 individuals, a female and her young-of-the-year. In other parts of the study area I found numerous signs of porcupine use of dirt burrows and deep washouts. Discussions with area ranchers

Table 1. Summer daytime resting cover of adult and juvenile porcupines in Harding County, S. D. based on 219 locations of 15 individuals.

COVER TYPE	NUMBER OF INDIVIDUALS	% OF TOTAL LOCATIONS
Shepherdia argentea	9	15.0
Mixed brush and forb species greater than 1.3 m high	10	11.4
Symphoricarpos occidentalis	8	13.6
Earth den	2	11.4
Grasses and forbs (excluding planted *Medicago sativa*)	8	10.4
Medicago sativa	6	6.8
Mixed brush and forb species less than 1.3 m high	5	6.4
In or under tree	6	5.0
Rock den or rock face	3	5.0
Artemesia spp.	3	4.1
Undercut creekbank	3	2.3
Rhus aromatica	2	2.3
Miscellaneous (deadfalls, *Crataegus*, etc.)	10	6.4

convinced me that porcupines living in dirt dens were a common occurrence. It is probable that the porcupine does not dig its own den or even alter existing ones. The only instances of digging by porcupines involved adults in extremely hot weather; they would scrape vegetation from damp earth in draws to form a shallow mold. Foxes (Vulpes fulva) and badgers (Taxidea taxus) are common in the study area and dig dens of a size useable by porcupines. Dens used by porcupines ranged in size from 25 to 35 cm in diameter at the entrance and were round to slightly oval. In three instances, porcupines occupied dens in active beaver (Castor canadensis) colonies in prairie creekbeds.

Many of the grass and forb location (Table 1) sightings were of juveniles just beginning to wander. This cover is a dense growth such as wheatgrass and sweetclover. Tall grasses provided visual concealment for porcupines, which in summer months have long, predominantly yellow guard hairs. Animals in this type of cover, especially in late summer and fall when grass had yellowed, were nearly invisible from as close as 2 m.

One facet of cover choice was the preference individuals exhibited for a particular type of cover. One animal would invariably be found in light, open, shallow cover, another in the thickest type of cover on its range, and another in mixed brush and tree species. Marshall et al. (1962) reported similar marked individual preferences for certain species of trees by adult porcupines.

Juveniles reflected the cover preferences of the mother. It was probable that the mother put her young in what she considered suitable cover before leaving it for the day, and from this perhaps the juvenile "learned" cover preference. All three of the mother-young pairs tracked for extended periods of time reflected this behavior.

Deadfalls and hollow logs, common cover types in other areas (Curtis and Kozicky 1944, Krefting et al. 1962), were scarce or absent in most of Harding County. The majority of trees in the draws were ash or willow, which do not have large trunks. Porcupine fecal deposits were occasionally found against banks beneath leaning trunks which gave some protection overhead and on one side.

The natal habitat of 2 porcupines was identified, the birth of one of these was witnessed. Birth occurred at 2130 hours under a large sagebrush (*Artemesia tridentata*) at the crest of a brush bank. The juvenile remained under the same bush for 3 days. It had some protection from the sun, but none from terrestrial predators. After 3 days it began crawling across and slightly down slope to heavier mixed cover, moving 1 to 3 m per night. The second young juvenile, less than a week old and still unable to walk well, was found in a dense thicket of buffaloberry. A number of old and fresh scats indicated the thicket had been in use by an adult for some time. The animal remained in the thicket for another 4 days before leaving. The location provided protection from weather and avian and larger terrestrial predators.

Food Habits

Grasses are of little dietary significance to porcupines except in early spring (March and April) when they average 10.0 percent of the diet (Table 2). Fifty percent of the animals examined during that period had eaten grass; the highest percentage eaten by any 1 individual was 89.0 percent. This early-spring move to grasses was also found in a study in the Modoc National Forest in California; animals collected in December had 100.0 percent coniferous stomach contents, but specimens collected in January had traces of grass, and in March specimens contained up to 60.0 percent grasses (California 1962). In Harding County another period of grass utilization occurred in November, when 41.0 percent of the individuals examined had eaten grasses; 7 different species were utilized with a maximum of 58.0 percent eaten by 1 individual.

Crested wheatgrass (*Agropyron cristatum*) occurred in samples from most months (Table 3). In summer the seedhead was usually consumed. Ricegrass (*Oryzopsis hymenoides*) occurred in 2 individuals in November; in 1 it constituted 58.0 percent of the dry weight of the stomach contents. This animal was collected in a lightly grazed pine savannah area with a good selection of shrubs, forbs, and trees.

In Harding County the cool season grasses are among the earliest plants to grow in spring, and the animals might seek green vegetation after a winter diet of shrub and tree bark. Sedges (*Carex* spp.) are common in the area and a frequent porcupine food elsewhere (Dodge 1967), but did not occur in any of the samples examined. This was

Table 2. Relative density (percent dry weight) of vegetation types in the diet of 81 porcupines from Harding County, S. D.

Sample period	N	Grasses Mean %	Grasses Range	Forbs Mean %	Forbs Range	Shrubs Mean %	Shrubs Range	Trees Mean %	Trees Range
January - February	13	0	0	1	0 - 6	52	3 - 97	46	3 - 97
March - April	16	10	0 - 89	20	0 - 99	9	0 - 49	60	0 - 99
May - June	6	1	0 - 4	39	0 - 73	53	24 - 96	7	1 - 20
July - August	17	1	0 - 9	25	1 - 98	64	1 - 98	10	1 - 70
September - October	4	2	0 - 4	25	9 - 56	63	24 - 90	9	1 - 18
November - December	25	3	0 - 58	12	0 - 59	29	0 - 88	56	2 - 100

Table 3. Species of grass in the diet of 81 porcupines from Harding County, South Dakota.

SPECIES	NUMBER OF INDIVIDUALS	SEASON(S)*
Agropyron cristatum	10	SP, LS, EW
Bromus inermis	3	SP, EW
Oryzopsis hymenoides	2	EW
Spartina pectinata	2	SP
Bouteloua gracilis	1	ES
Elymus virginicus	1	EW
Phalaris arundinacea	1	EW
Secale cereale	1	EW
Stipa comata	1	SP
Stipa viridula	1	SP
Winter wheat	1	EW
Unidentified species	12	SP, F, EW

*Seasons: ES (early summer), May and June; EW (early winter), November and December; F (fall), September and October; SP (spring), March and April.

unexpected, since needleleaf sedge (C. *eleocharis)* is one of the first plants to green in spring (Johnson and Nichols 1970). Winter wheat may play a greater role in the diet than was shown by the results; ranchers in the area reported seeing porcupines grazing in winter wheat fields in late fall and early spring. Spencer (1946) commented on the problem of Colorado porcupines wallowing down ripening wheat when feeding, and Johnson and McBee (1967) collected porcupines in wheat fields in Montana.

Year-round mean dry weight of forbs in the diet was 20.5 percent (Table 2). Peak season for forbs was early summer (May-June), late winter was the low season. The maximum number of forb species (12) occurred in July-August, followed by November-December with 8. Alfalfa was the most commonly eaten forb (Table 4). Many of the species listed in the table constituted a large portion of the meal, even though they may have been eaten by only one individual, and thus cannot be considered accidental. Various species of vetch *(Astralagus* spp.) were common in the study area but were not eaten; however, porcupines in captivity will eat vetch (Taylor 1935).

Alfalfa was the primary forb species eaten in all periods. There may have been a bias towards a higher percentage of alfalfa in the diet than may actually occur, since many porcupines were collected along roads where alfalfa mixtures had been planted. Ranchers left haystacks standing in fields through the winter, and porcupines often used these stacks as dens.

Wild licorice *(Glycyrrhiza lepidota)* was the second most commonly

Table 4. Species of forbs in the diet of 81 porcupines from Harding County, South Dakota.

SPECIES	NUMBER OF INDIVIDUALS	SEASON(S)*
Medicago sativa	52	LW, SP, ES, LS, F, EW
Glycyrrhiza lepidota	20	LW, SP, ES, LS, F, EW
Melilotus officinalis	14	LW, ES, LS, EW
Dalea enneandra	11	EW, LW, LS
Chrysopsis villosa	7	ES, LS, F, EW
Artemesia cana	4	LW,. SP, LS
Oxytropis spp.	3	ES, LS
Artemesia tridentata	2	LS, EW
Calomovilfa longifolia	1	SP
Cleome serrulata	1	LS
Gaura coccinea	1	LS
Lesquerella spp.	1	EW
Sphaeralcea coccinea	1	LS

*Seasons: EW (early winter), November and December, ES (early summer), May and June; F (fall), September and October; LW (late winter), January and February; LS (late summer), July and August; SP (spring), March and April.

eaten forb species (Table 4); 20 of the 81 animals used it. Wild licorice was most frequently consumed during July-August when it also served as daytime resting cover. There was a second peak of licorice in the diet during November. Wild licorice grows in fairly thick, high (0.5 to 1.0 m) clumps and may be one of the few forbs to remain standing in fall and winter.

Yellow sweetclover (*Melilotus officianalis*) was eaten by 14 individuals. It is more widely distributed than licorice, because it is used as a hay crop in Harding County and has been planted along roadsides and in many pastures. Use of haystacks as winter dens may contribute to the high incidence of sweetclover in winter diets. It is a thick tall forb and remains standing late in the season.

Narrowleaf goldenaster (*Chrysopsis villosa*) was eaten by porcupines primarily during summer months, when greater succulence may make the rough stems and leaves more palatable. It is a perrenial forb which reaches 0.5 m in height (Van Bruggen 1976) and may be available in dried form during winter months. Levels in the diet ranged from less than 1.0 percent to nearly 90.0 percent of a sample.

Bigtop dalea (*Dalea enneandra*) was a major item in porcupine diets in late summer and fall. This was expected because this forb was primarily found on ridgetops and hillsides (Johnson and Nichols 1970), and porcupine movements were primarily in draws. Dalea is a tall (0.3 to 1.0 m) plant, but has a light structure and may not remain standing in winter.

Locoweed (*Oxytropis* sp.) occurred in fecal samples from 2 juveniles sampled in July, and 1 adult in June. These individuals were radiotagged and appeared to remain in good health for 3 weeks afterward, even though locoweed composed 59.0 percent of the dry weight of the adult's feces and was the only forb eaten. Locoweed may not be addictive to porcupines as it is to livestock, occasional feeding apparently does no harm. Porcupines are caecal animals. Much of the poison in the plant may not be released until the majority of the intestine has been passed; therefore a caecal animal would absorb a smaller quantity than a ruminant would. Range conditions are good in the study area, it is not likely porcupines are forced to eat this species because of lack of other forage.

Three species of sage were eaten. Due to their height and woody structure, sages are exposed even during relatively deep snow. Sages were also used as a daytime resting cover by both adults and juveniles. Taylor (1935) lists silky wormwood (*Artemesia dracunculus*) as one of the species accepted by captive porcupines. The most frequently eaten species of sage, silver sagebrush (*Artemesia cana*) increases with cattle grazing pressure (Johnson and Nichols 1970); incidence in porcupine diets may increase with drought and resultant overgrazing.

Shrubs formed the major portion of the diet from May through October and in January and February (Table 2). The lowest shrub use coincided with peaks in grass and tree use in early spring. Parts of shrubs eaten were leaves, terminal shoots, fruits, and inner bark. Inner bark was eaten primarily during winter months. Lower portions of shrubby species are not debarked or eaten, possibly for nutritional reasons. Mid- and butt sections have lower crude protein levels than stem tips, while terminal segments of shrubs are more digestible than those of older tissue (Dietz 1972). Shrubs are not considered a good source of energy after fruit development (Cook 1972), which may explain the high quantity of fruits and berries in porcupine diets. Fruits occurred in 64.0 percent of the samples and were eaten all months of the year. Species could not be identified, but those most available were buffaloberry, hawthorne, gooseberry (*Ribes missouriense*), snowberry, wild plum (*Prunus americana*), skunkbrush, wild rose, and wild cherries (*Prunus* spp.).

The most important shrub species was buffaloberry (Table 5), eaten by all age-groups throughout the year. Terminal twigs, bark, leaves, and berries were consumed. Eighty-five percent of the samples examined contained buffaloberry; in many cases it comprised the greatest percentage of stomach or fecal contents. The shrubby, spreading nature of buffaloberry made it easy for juveniles to climb; they were often found in the lower branches in late afternoon, feeding on leaves and small young twigs. Porcupines feed on buffaloberry in both Oregon and North Dakota (Taylor 1935).

Hawthorne was eaten by over 25.0 percent of the porcupines samples. One radiotagged inJividual spent 3 continuous days in a small hawthorne patch. One day snow was falling lightly and he was climbing in small branches about 3 m above the ground, eating berries. Tracks showed he had pawed through the 5 cm deep snow to reach fallen berries.

Table 5. Species of shrubs in the diet of 81 porcupines from Harding County, South Dakota.

SPECIES	NUMBER OF INDIVIDUALS	SEASON(S)*
Shepherdia argentea	68	LW, SP, ES, LS, F, EW
Fruit (unknown species)	52	LW, SP, ES, LS, F, EW
Crataegus sp.	23	LW, SP, ES, LS, F, EW
Rhus aromatica	4	EW
Rosa spp.	1	LW
Symphoricarpos occidentalis	1	LW
Unknown shrub species	2	LW

*Seasons: ES (early summer), May and June; EW (early winter), November and December; F (fall), September and October; LW (late winter), January and February; LS (late summer), July and August; SP (spring), March and April.

Five species of trees were identified in the diet (Table 6). Ponderosa pine (needles, inner bark, and strobili) was eaten more than any other tree species. Animals in winter prairie dens several kilometers from pine had traces of pine in fecal or stomach contents. Pine usage varied from 100.0 percent of the individuals in the January-February period to 30.0 percent of all individuals in the May-June period. However, the actual quantity of pine was low. In late winter the total mean dry weight of all tree species in the diet was only 46.0 percent of stomach or fecal contents. Determining actual pine usage in the diet was complicated by the fact that pine is more easily identified than other tree species and the smallest fragments could be recognized.

Thirty-eight percent of all porcupines sampled had eaten willow (*Salix* spp.). It often constituted a large proportion of the tree species found in a sample. No seasonal variation in feeding intensity was noted, although the part of the plant utilized changed. Bark and terminal twigs were eaten in winter, buds and new leaves in summer.

Sixteen individuals (20 percent) fed on green ash. Bark of larger limbs and trunks was never chewed, but terminal limb portions were found debarked. The actual quantity eaten was small; ash was rarely the most abundant tree species in the sample. Green ash was the most common tree in prairie draws, and low levels in the diet indicated low palatibility. In areas where willow or poplar were abundant, signs of feeding on ash were scarce or absent. Some seasonal preference was noted; 69.0 percent of the samples with ash

Table 6. Species of trees in the diet of 81 porcupines from Harding County, South Dakota.

SPECIES	NUMBER OF INDIVIDUALS	SEASON(5)*
Pinus ponderosa	65	LW, SP, ES, LS, F, EW
Salix spp.	31	LW, SP, ES, LS, F, EW
Fraxinus pennsylvanicus	16	LW, SP, LS, F, EW
Populus spp.	7	LW, F, EW
Ulmus spp.	6	LW, EW
Unknown species	5	LW, SP

*Seasons: ES (early summer), May and June; EW (early winter), November and December; F (fall), September and October; LW (late winter), January and February; LS (late summer), July and August; SP (spring), March and April.

came from November and December.

Poplar and cottonwood trees were utilized by 9.0 percent of the individuals. Fall and winter were the only seasons poplar bark was utilized. Unlike patterns of porcupine feeding on ash, poplars were debarked all along the trunk and near-vertical branches, resulting in the baring of long sections of the trunk and upper surface of branches. Poplar trees felled by beavers or creek washouts were frequently utilized by porcupines, often to the point of stripping the downed or leaning tree of its bark. Most downed trees of this genus had bark eaten and the casual observer would assume porcupine feeding was the cause of the tree's death rather than the result of it. This may have led to some additional undeserved landowner animosity toward porcupines.

Poplar bark remains palatable for some time after the tree falls. One large tree, downed prior to March 1976, had had an adult female feeding on it for some time. She remained in the vicinity, and her juvenile of that year was found feeding numerous times on the remaining bark of the same tree in January 1977.

Cottonwood is a common porcupine food item in desert areas. Porcupines in parts of Arizona utilize cottonwood groves along the Colorado River (Monson 1948, Pulich 1953). Porcupines were also once common where cottonwood grew in Kansas, along the Smoky, Solomon, and Republican Rivers and tributaries, and also in hills of northwestern Kansas where cottonwood trees were found (Hibbard 1934).

Elm (*Ulmus* spp.) bark and wood were found in 7.0 percent of the samples, all from winter. Porcupines in New England eat new leaves and buds of elm in early spring (Dodge 1967), but evidence of this was not found during winter surveys. Either instances were scarce, or the damage was not readily visible.

Feeding Trials

Digestibility of components of alfalfa and pine inner bark by captive porcupines and proximate analysis of the components are shown in Table 7. Pine bark contained only 3.2 percent protein. Deer require a minimum of 7 percent protein in the diet (Dietz 1972); a non-ruminant such as a porcupine would require higher levels, particularly if pregnant. The addition of needles and stem tips to the pine bark diet would probably add little protein; jack pine (*Pinus banksiana*) browse contains only 3.8 percent protein (Ullrey et al. 1967). The digestibility of crude protein was -35.78 percent (Table 7); porcupines excreted more nitrogen (reported as crude protein) than they consumed. Alfalfa was high in protein (more than 20 percent), which might be one reason it was heavily utilized in winter. Ponderosa pine was 20.6 percent higher in ether extract and 14.9 percent higher in nitrogen-free extract than alfalfa, and thus appeared to be higher in energy. These high values might be due to pine resins, turpenes, oils, and other similar substances of little nutritional value.

Porcupine assimilation efficiency for alfalfa (77.6 percent) was lower than the 83.6 percent for pine (Table 8), possibly due to

Table 7. Analysis of vegetation consumed (expressed as means of composited samples) and digestibility of proximate fractions in porcupine feeding trials.

VEGETATION	CRUDE PROTEIN (%)	CRUDE FIBER (%)	ETHER EXTRACT (%)	NITROGEN-FREE EXTRACT (%)	ASH (%)	TDN (%)	ESTIMATED* ENERGY kcal/g
Ponderosa Pine							
Forage	3.18	12.38	22.35	60.71	1.38		4.33
Digestibility (z)	-35.78	80.60		86.57			
SD	90.31	5.45		8.61			
Alfalfa							
Forage	24.00	19.10	1.74	45.85	9.31	73.13	3.85
Digestibility (x)	76.19	67.94		85.02			
SD	5.85	4.63		1.67			

*Calculated using values of 4.5 kcal/g for protein, 4.0 kcal/g for carbohydrates, and 9.5 kcal/g for fat.

Table 8. Forage consumption, assimilation efficiency, and energy expenditure of porcupines on pine inner bark and alfalfa diets.

	PINE	ALFALFA
Forage consumption (dry weight), g/kg/day		
mean	7.60	9.62
SD	6.89	5.42
Assimilation efficiency (ash-free)		
mean	83.60	77.64
SD	11.38	1.18
Forage digested, kcal/kg/day*		
mean	29.37	25.92
SD	28.93	14.29
Fat utilization, kcal/kg/day**		
mean	108.77	80.00
SD	51.09	56.08
Total energy consumed, fat + forage, kcal/kg/day		
mean	138.14	119.20
SD	74.77	57.33
Resting metabolic rate (RMR), kcal/kg/day***		
mean	39.99	40.58
SD	3.43	2.00
Cost of stress and activity, kcal/kg/day		
mean	98.14	78.71
SD	71.46	56.30
Energy expenditure of active animal		
mean	3.35 x RMR	2.92 x RMR
SD	1.49	1.14

* From Table 7.
** 1 gram of fat util'zed = 9.5 kcal.
*** RMR = 64.67 W_{kg} 0.17 (Fig. 5).

slightly higher levels of crude fiber in alfalfa. Assimilation efficiencies of other herbivores from the North Plains ranged from 72.0 percent to 93.0 percent (Johnson and Groepper 1970). Porcupines digested 6.7 g/kg per day on both rations. Weight losses and total energy consumption were higher for animals on a pine diet. Part of the extra energy expenditure may have been due to the tendency of porcupines to manipulate the pile of pine logs in each cage. Maintenance energy expenditures increased 3.8 to 4.8 times predicted basal metabolic rates when exercise wheels were supplied to rodents in a study by Johnson and Groepper (1970). Maintenance energy requirements of rodents without exercise wheels were 1.6 to 4.0 times estimated basal metabolic rates.

Age and Sex Ratios

Eighteen (33 percent) of 55 skulls from Harding County were young-of-the-year (Fig. 4). There was a sharp drop to the 1-year-old age-class (8 individuals). Forty-nine percent of the population was in the 2- and 3-year-old age-groups, and only 2 individuals (4 percent) survived to 4 or more years. Brander (1971) reported that porcupines can live over 10 years in the wild. The lack of older age-classes in Harding County indicated a high adult mortality rate. A female porcupine does not breed until her second fall, and thus does not give birth before 2 years of age. If the majority of the animals are dying before their 4th year, a female has at most 2 seasons to reproduce herself and a portion of the polygomous

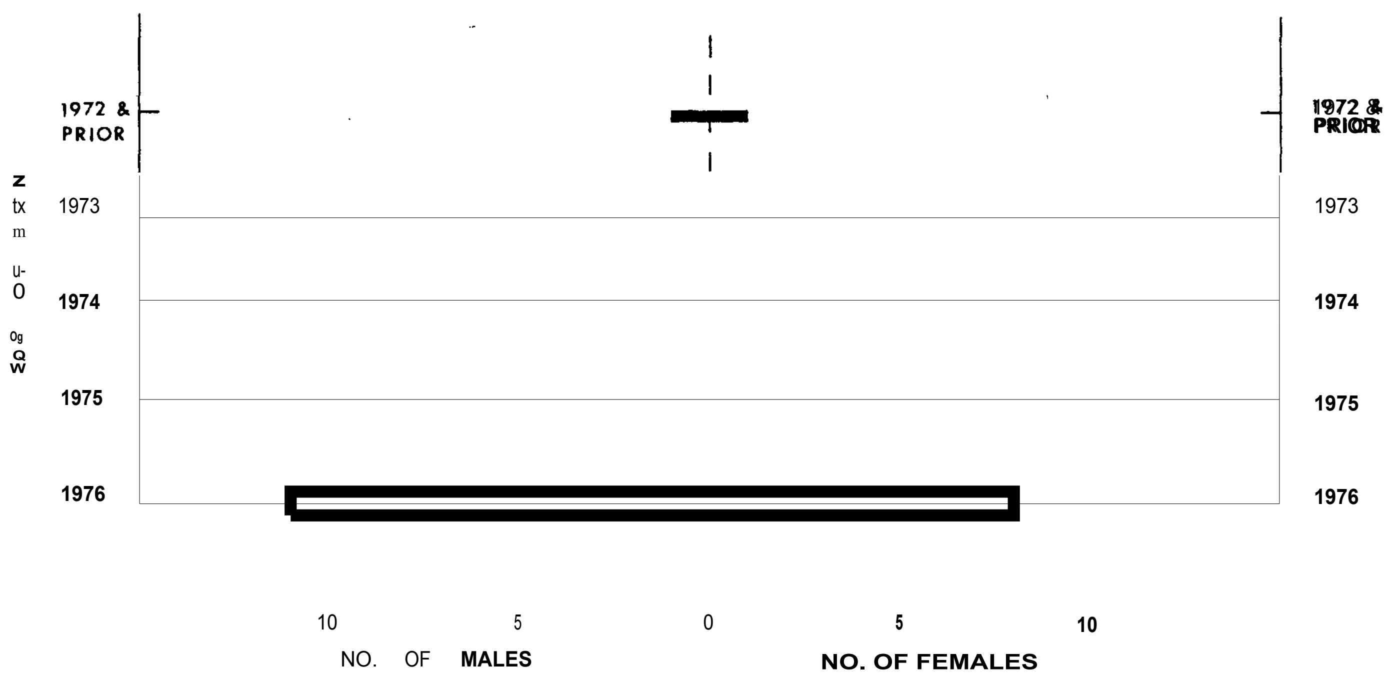


Figure 4. Age ratios of male and female porcupines captured in Harding County, S.D.

male population. This leaves little margin for juvenile mortality. This high mortality of the 1975 age-class could not be explained. An unusually early and severe blizzard in November 1975 may have killed a number of juveniles that had not yet moved to dens and had low fat reserves because of growth.

Of 174 animals captured, 120 were adults and 54 were young-of-the-year. The population was 34.5 percent adult male, 16.0 percent juvenile males, 34.5 percent adult females, and 15.0 percent juvenile females. The sex ratio among adults was 100:100 males to females, and 100:93 among juveniles. However, the apparent sex ratio of the population varied with season due to changes in behavior associated with reproductive activity. Between February (late pregnancy) and July (weaning), female captures exceeded male captures every month except April, and the apparent sex ratio was 100:147 males to females. During breeding season, from August through December, the capture of males exceeded capture of females in all months except November, and the apparent adult sex ratio was 100 males to 64.5 females. In spring and summer females have a home range and daily movement pattern almost three times greater than males and thus are exposed to capture more during this period. In fall when males are reproductively active and the energetic demands on females are lower, movement patterns reverse, and males become more susceptible to capture.

Reproduction and Growth Rates

Fifty-four young of the year were captured per 60 adult females, indicating a high reproductive rate and survivability of young. Eleven (100 percent) of the adult females autopsied in December 1976 and January 1977 were pregnant, 12 of the 18 females examined in July 1976 were lactating. Of the 6 non-lactating females, 5 weighed approximately 2 kg less than the mean for the lactating group and were probably yearlings.

Scrotal males were found beginning in June 1976. By September, 67.0 percent of the adult males were scrotal. In July mean weight of scrotal males was 11.1 kg, and mean weight of non-scrotal males was 9.1 kg. In August the mean weights for scrotal and non-scrotal males were 9.6 and 7.0 kg, and in September mean weights were 10.0 kg (scrotal) and 7.6 kg (non-scrotal). Older age-groups apparently become reproductively active first, followed by younger males. Larger males can be assumed to be older, since porcupines show a definite age-weight correlation (Dodge 1967). Generally, porcupines do not breed until their second fall, but three scrotal juveniles, one only 4 months old, were found between September and December. In August, an apparently sterile male was captured; its testes were abdominal and approximately 1/5 normal size.

Birth dates of 8 wild-bred porcupines ranged from April 19 to June 10. The gestation period of porcupines is 210 days (Shadle 1951), placing conception dates between September 21 and November 13. Dodge (1967) determined the peak of spermatogenisis to be in early October, which coincides with the majority of conception dates.

The mean birth weight of 8 lab-born porcupines was 581 grams (range 507-680 g). One juvenile born in the wild weighed 450 g. The instantaneous relative growth rate (IGR) was calculated with the formula:

$$IGR = \frac{\text{in } W2 - \text{in } W1}{T_2 - T_1} \quad (7)$$

(Brody 1945). IGRs were highest in the first week of life, declined rapidly for the first month, then slowly decreased until fall, when colder temperatures and/or lower food quality prevented growth. The highest IGRs recorded were 0.039/day for a wild juvenile and 0.059/day for a lab porcupine. These growth rates were similar to those of animals which reach maximal body weights slowly, i.e. cattle, which have a growth rate of 0.04. Typical IGRs of fast-maturing rodents are 0.71 (mice), 0.53 (rats), and 0.22 (guinea pigs) (Brody 1945).

The energy cost of growth was determined on a 1-week old female with an IGR of 0.047/day (38 g/day). Her resting metabolic rate was 136.3 kcal/kg per day, double the predicted resting rate of 72.5 kcal/kg per day (Fig. 5).

Laboratory porcupines had lower growth rates initially, but IGRs did not decline as steeply, resulting in larger animals (up to 6 kg) by fall. The IGRs of lab juveniles were slightly above 0.01/day in late August, when IGRs of wild juveniles had dropped to less than 0.005/day. Wild juveniles weighed 30-50 percent less in September than lab-reared porcupines of the same age-group. The smaller birth weight and growth rates for wild juveniles were probably due to differences in nutrition. Forced close proximity of the mothers in the lab allowed frequent daytime feeding, which was not possible for wild juveniles. High-energy, high-protein feed was provided ad-libitum to pregnant and nursing females and weanling juveniles.

Energy Requirements and Temperature Regulation

The resting metabolic rates (RMR) of 8 barren adult females, 1 adult male, 1 lactating female, and a 1-week-old juvenile female were determined. The mean RMR of non-reproductive adult porcupines was 40.75 kcal/kg per day (range 31.5 - 48.6 kcal • kg^{-1} day^{-1}, SD 2.37). There was no difference in RMR between sexes or between the lactating female and non-lactating females. Regression of daily consumption in kcal on porcupine body weight gives a line described by the equation:

$$RMR = 4.17 + 0.767 \log W(kg) \quad (8)$$

($r = 0.78$, $P < 0.0005$). This can be reexpressed as:

$$RMR = 64.67\ W(kg)^{0.767} \quad (9)$$

(Fig. 5), which is slightly lower than predictive formula for mammals, 70 $W(kg)^{0.75}$ (Brody 1945). The lower rate is not unexpected, as most rodents studied appeared to have metabolic rates below predicted for mammals in general based on body weight (Baudinette 1972). Irving et al. (1955) obtained a higher rate, 45 kcal/kg/day, (data transposed from graph) on Alaska porcupines. The difference may be due to sample size; Irving tested only 4 individuals.

Metabolic rates of porcupines in summer pelage began to increase between 20 and 25 C. The first sign of increased metabolic rate was

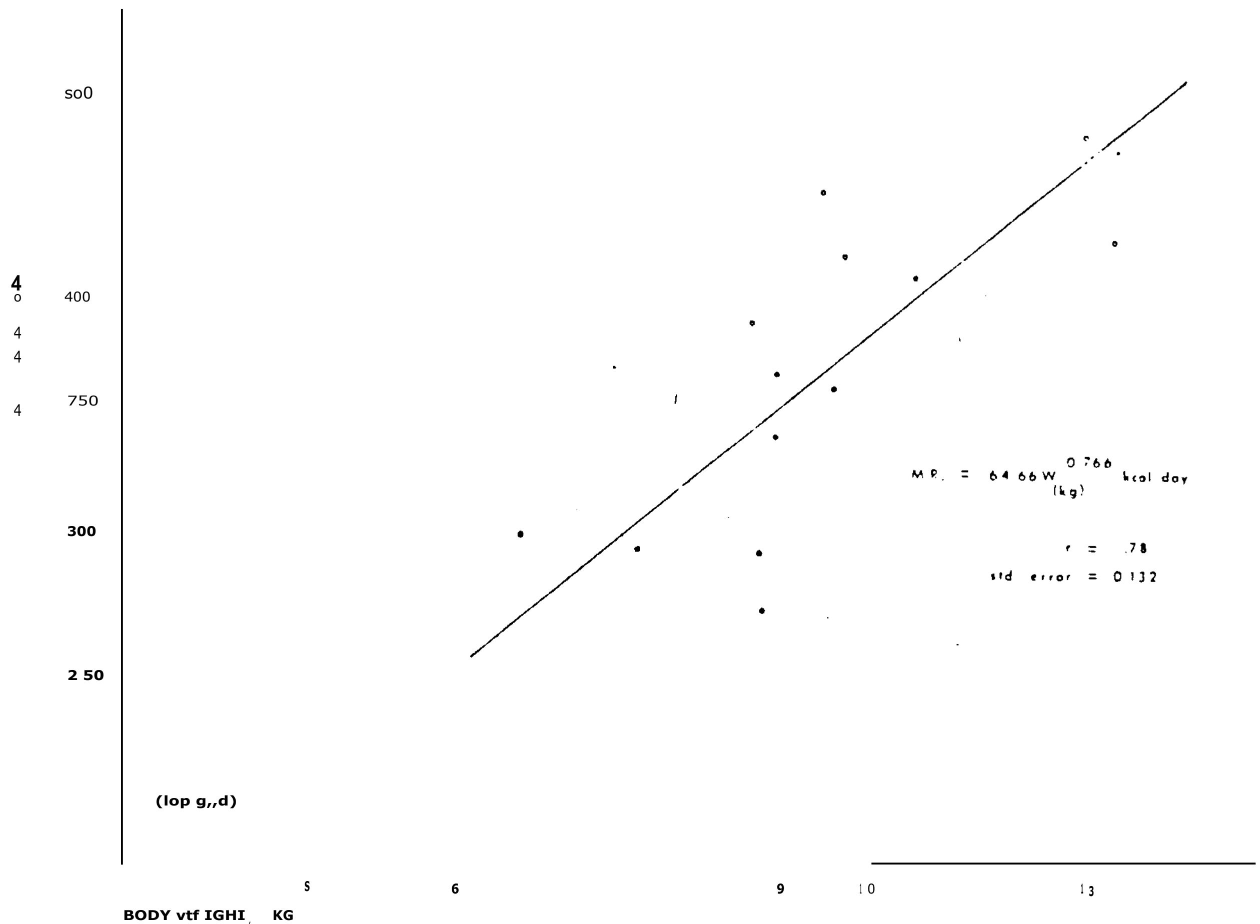


Figure 5. Resting metabolic rate of porcupines in thermoneutrality (16 - 20 C

restlessness in the metabolic chamber, followed by rises in body temperature and increasing breathing rates. Increased metabolic rate with increasing ambient temperatures followed the regression equation

$$Y = 15.24 + 1.15\ X \tag{10}$$

where Y is the metabolic rate in kcal • kg^{-1} day^{-1} and X is ambient temperature in degrees C (Fig. 6). The upper critical temperature (UCT) appeared to be between 20 and 25 C. This seemed to be an unusually low UCT but the animals showed a definite restlessness which I attributed to discomfort. At 35 C the animals were panting heavily and alternating between complete prostration and struggles to escape the chamber. When removed from the chamber most individuals immediately spread flat on the cool floor for several minutes. Ventral surfaces of porcupines are scantily haired in summer and there may be considerable cooling of body temperature through conduction. Similar behavior by wild porcupines was noted on hot days in Harding County; animals would scrape vegetation from damp earth in draws, or take shelter in earth or rock dens where temperatures were several degrees cooler than on the surface.

Porcupine body temperatures were unstable, varying with ambient temperature, muscular activity, and excitement. Deep body temperature of inactive porcupines at thermoneutrality was 37.1 C (range 36.5 - 37.6 C). This was lower than what was measured by Dodge (1967) but agrees with Irving and Krog (1954), who obtained a mean temperature of 37.5 C (range 37.0 - 38.2 C).

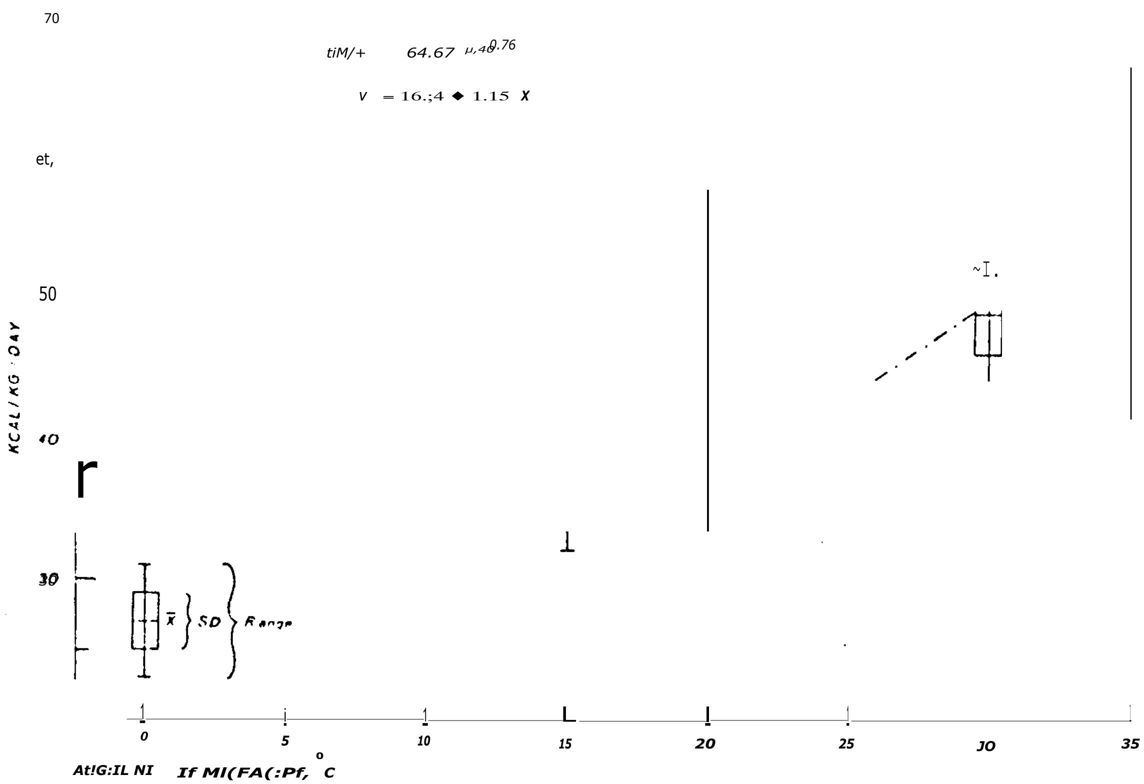


Figure 6. Resting metabolic rate of adult porcupines in summer pelage.

Body temperatures of porcupines in summer pelage rose an average of 1.7 C within 1 hour of exposure to ambient temperatures of 30.0 C, and within 1 hour of exposure to 35.0 C rose 2.4 C above initial body temperature. Porcupines with body temperatures around 40.0 C panting heavily and often layed flat on cool surfaces. Juveniles appeared to be less tolerant to high temperatures than adults.

The extent of body temperature fluctuation over a 24-hour period depended on ambient temperature. Near the low end of the thermoneutral zone (-9.0 C) body temperatures were stable, varying only 0.9 C over 24 hours (N = 3). However, at the upper end of the thermoneutral zone (23.0 C) body temperatures varied as much as 1.6 C (Fig. 7).

Porcupine reactions to hear may be similar to those of the belding ground squirrel (*Spermophilus beldingi*), which does not maintain thermal equilibrium for long periods of time; body temperatures fluctuate over a range of 3-4 C to reduce metabolic costs of maintaining a high body temperature (Morhardt and Gates 1974). Body temperatures of porcupines were slightly higher during nightime hours than during the day. This small rise during active periods was probably due to restlessness in the small testing chamber.

Several heat waves occurred in summer 1975, when daytime temperatures were near 35 C for several days. Porcupines in the laboratory were kept in shaded outdoor pens with ample water; however, in the days following extended periods of unusual heat several animals died. Two adults died of *Bordetella* pneumonia, which is

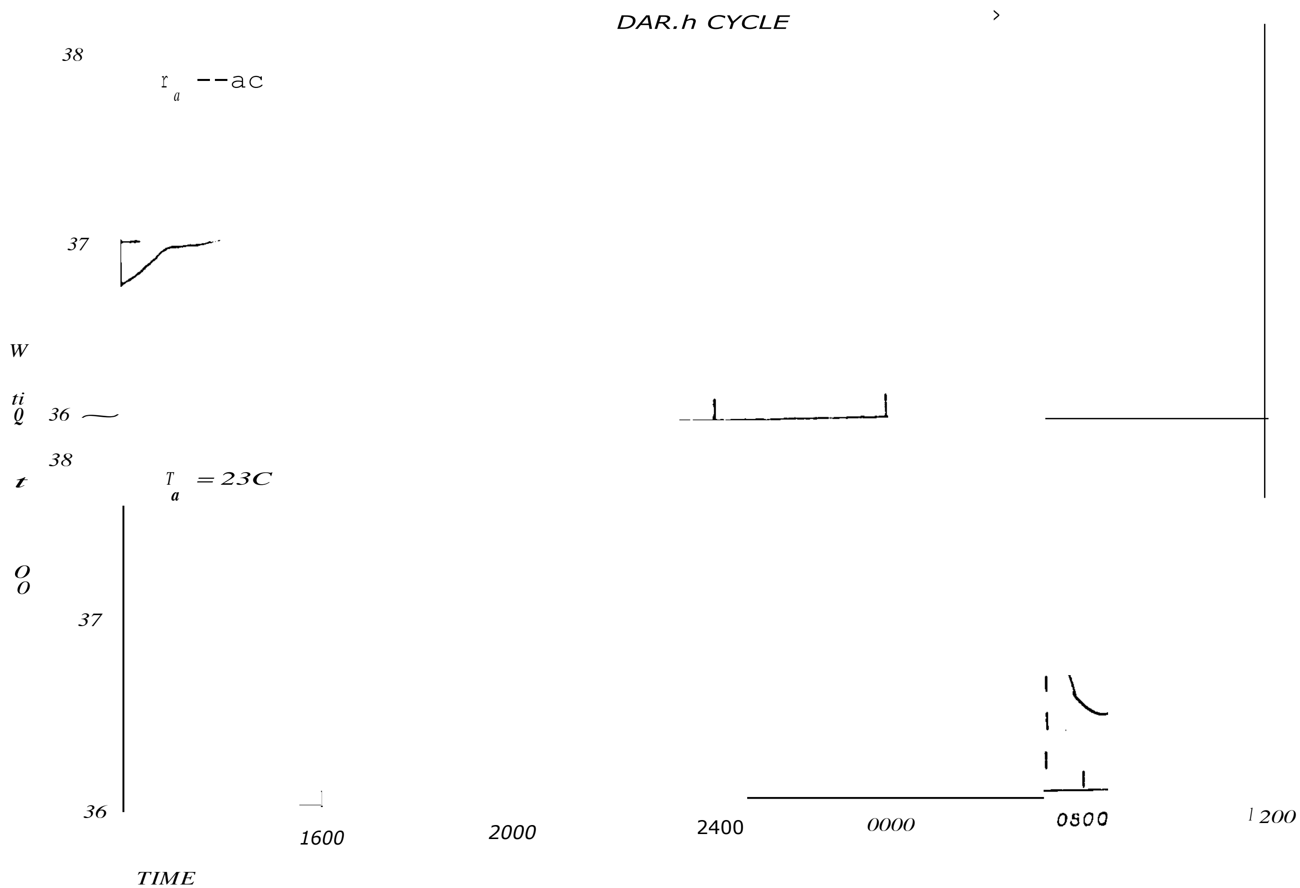


Figure 7. Variations in adult porcupine body temperatures over 24 hours (n = 3).

generally predisposed by stress (personal communication, D. Nelson, South Dakota Veterinary Diagnostic Laboratory), and two died of starvation. Starved animals had been in captivity for nearly a year; they stopped eating during the heat wave and refused further food. Abnormally high body temperatures can result in reduction of oxygen transport by the blood pigments, increased permeability of cells, and enzyme inactivation or breakdown (Prosser 1973). It was possible that prolonged high body temperatures caused temporary physiologic or neurogenic damage which predisposed the porcupines to infection or abnormal behavior. In a hot climate, protection from heat during summer may be more essential to porcupine survival than protection from cold in winter.

Mortality and Disease

The Harding County porcupine population was generally healthy; 9 of the 192 individuals examined showed outward signs of disease or injury. Mortality related to human presence was high, particularly among juveniles. Of the 5 young tracked during summer 1975, 3 died of man-related causes (traffic or shooting), and an additional one would have been shot if not clearly marked as an experimental animal. Of 6 adult telemetry females, one was ill when last seen and probably died, another would have been shot if not clearly marked. Of 3 adult males, 1 was killed by traffic and 1 was injured. These man-related mortalities are not doubt higher than for the general population, because only individuals which occasionally came near the road were used for telemetry. Farther from the road, traffic deaths were not a factor, but most ranchers and hunters in Harding County shoot all those they see.

Several abnormalities were found during autopsy. The kidneys are normally directly opposite each other but in 11 porcupines the right kidney was 0.5 to 2.0 cm anterior to the left. The left kidney was never anterior to the right. Two types of heart abnormalities were found in this population. One juvenile approximately 4 months old had equal-sized ventricles and an intact, but closed, 0.75 cm long pulmonary-aorta shunt. In 8 porcupines the ventricles were externally equal in size, giving the heart a square appearance. In these cases the right ventricle wall was thicker than the left, so that the interior space was very small.

The most common internal parasite of Harding County porcupines was the roundworm *Wellcomia evaginata,* which was found throughout the large and small intestines. Dodge (1967) found this parasite to be common in Massachusetts porcupines. Tapeworms *(Monoecocestus variabilis)* were occasionally present. Parasite migration tracts and nematode ova were sometimes found in the liver. In one case the liver was completely covered with granulomas surrounded with a zone of neutrophilic inflammation, and numerous parasite eggs were present in the granulomas.

External parasites included lice, ticks and fleas. Porcupine lice *(Trichodectes setosus)* were found on all animals, with heaviest infestations occurring in winter. Tick *(Dermacentor andersoni)* infestations reached highest concentrations in late spring, with another smaller peak in fall.

Two species of fleas have been recorded on porcupines, Ceratophyllus wickhami and C. adustus. These were not found in Harding County, but 2 males collected in December 1977 carried Arctopsylla setosa, which infest various genera of carnivorous animals in the northwestern United States and Canada (personal communication, B. McDaniel, Entomology-Zoology Department, South Dakota State University). The recorded hosts for this species of flea in the United States are coyote (Canis latrans), black bear (Euarctos americanus) and cougar (Felis concolor), all from Montana. The most likely host in South Dakota which would be a possible source for infecting porcupines would be coyotes. An ongoing coyote parasite study in Harding County has found no infestation of A. setosa on coyotes (personal communication, E. Sheldon, Wildlife and Fisheries Science Department, South Dakota State University). The infestations were probably not temporary, since there were several dozen fleas, both males and gravid females, on the porcupines. The source of the infestation may have been previous carnivore occupants of earth or rock dens utilized by porcupines.

Laboratory colony porcupines were susceptible to numerous infections, primarily by bacterial origin. The source of pathogens in many cases was undoubtedly contact with rats and mice which frequented the outdoor cages. Enteritis was a common problem, particularly before a suitable ration could be developed. A too-rich diet lacking in roughage was the probable cause in several cases of enteritis. The addition of hay and wood, and decrease in grain, was helpful. It was important to begin feeding oral antibiotics to all colony animals as soon as signs of diarrhea were discovered, since one of the first symptoms of disease in porcupines is loss of appetite. Injectibles tended to be less effective and caused trauma to the animals from handling.

Several pneumonia-caused deaths occurred. Two cases were caused by Bordetella sp., 1 by Pseudomonas sp., and 1 by inhalation of foreign material. Enteritis deaths were caused by Salmonella (3 individuals), Aeromonas hydrophila (1 individual), and a nematode infection {1 individual).

One adult and 1 subadult became ill at the same time in midwinter with an identical paralysis of the posterior half of the body. The cause was an abcess of a thoracic vertebra, with resulting osteomyelitis and compression of the spinal cord. The causative bacteria could not be isolated from the abcess, but a Pasteurella organism was present in the lungs and intestines, and is known to cause multiple abcesses in other species (personal communication, D. Johnson, South Dakota Veterinary Diagnostic Laboratory). A third case of paralysis was caused by bacterial spinal meningitis. Salmonella sp. was isolated from the spleen and Erysipelothrix insidiosa from the muscle tissue of the hind leg.

Taxonomic Characteristics

Mean external measurements of 52 adult male porcupines from Harding County, S. D. were: total length, 704 mm; tail, 187 mm; hind foot, 91 mm; ear, 20 mm. Forty-nine adult females measured 653-164-83-20 (Table 9). The type male of the subspecies, E. *dorsatum bruneri* Swenk, measured 797-202-117, and measurements of the paratype female were 865 (including tail hairs)-199-98 (Swenk 1916). External measurements of the type and paratype animals were within the range of the Harding County group, with the exception of hind foot length of the type male, which was longer than the maximum for Harding County (115 mm). The mean weight of 101 Harding County adults was 7624 g (Table 9), which was larger than other populations studied (Curtis and Kozicky 1944, Krefting et al. 1962), and was consistent with the description of E. d. *bruneri* as larger than other subspecies (Swenk 1916).

Harding County specimens did not contradict the original description of the coloration of the subspecies E. d. *bruneri* (Swenk 1916). The general color tone of Harding County adults was the greenish-yellow of the western subspecies (E. d. *epixanthum*) rather than the rusty- or orange-yellow of E. d. *myops* and E. d. *nigrescens* described by Anderson and Rand (1943). The coloration of Harding County specimens was highly variable, ranging from nearly black to completely yellow, and changed in individuals with season and age. The underside of the tail was a distinct brownish-yellow, as described by Swenk (1916) for E. d. *bruneri*. The grey legs of the paratype

Table 9. External measurements and weights of adult* porcupines collected in Harding County, S. D.

	N	MEAN	RANGE	STD. DEV.	"F"
Total length (mm)					
males	52	704.4	540 - 874	154.623	
females	49	653.7	595 - 753	141.933	
total	101	679.8		150.030	P<0.090
Tail length (mm)					
males	52	187.6	134 - 250	45.350	
females	49	164.5	135 - 220	39.215	
total	101	176.4		43.845	P<0.007
Hind foot length (mm)					
males	52	91.4	73 - 115	21.442	
females	49	83.6	70 - 107	19.358	
total	101	87.6		20.725	P<0.060
Ear length (mm)					
males	52	20.4	15 - 30	5.322	
females	49	20.2	14 - 30	5.665	
total	101	20.3		5.465	n.s.
Weight (g)					
males	52	8090.8	5000 - 15000	369.95	
females	49	7129.4	5000 - 11800	312.26	
total	101	7624.4		246.89	P<0.512

* 1 year or older

immature female described by Swenk were rare, although many specimens had grey cheeks or foreheads. No albinos or partial albinos were seen. Two reddish-brown individuals were captured.

Coefficients of variation for cranial measurements ranged from 3.0 to 13.4 (Table 10). Cockrum (1954), working with *Peromyscus* from Kansas, stated that cranial measurements with coefficients of variation (C.V.) from 3.1 to 4.1 are of questionable value for taxonomic studies and measurements with a C.V. greater than 4.1 are too highly variable to show significant geographical variation, at least for the species and area concerned. For Harding County porcupines, only the zygomatic width had a C.V. under 3.1, and only skull length (C.V. 3.8) was within the "questionable" range. All other measurements had a C.V. between 4.4 and 13.4. Considerable variation of cranial bones between individuals may be a species characteristic. Anderson and Rand (1943), working with Canadian porcupines, also observed great individual variation. A larger sample size from Harding County thus might not have reduced the C.V. to standards applicable to other species.

Anderson and Rand (1943) selected 4 cranial measurements as the most useful for comparisons of porcupine skulls: condylobasal length, zygomatic breadth, length of nasals, and width of rostrum. None of the Harding County skulls were as long as the 115.5 mm E. d. *bruneri* type skull (Swenk 1916). Harding County skulls ranged from 88.1 to 111.6 mm (Table 10). The zygomatic breadth of the type male was 73 mm, close to the mean of Harding County males (72.4 mm). Nasal

Table 10. Skull measurements of adult porcupines collected in Harding County, S. D.

MEASUREMENT	N	MEAN (mm)	STD. ERROR	RANGE	"F" BY AGE	"F" BY SEX	COEFFICIENT OF VARIATION
Mandibular length							
males		76.4	0.859				
females		71.1	0.940				
total	31	73.8	0.612	63.6 - .82.4	P < 0.005	P < 0.05	4.6
Mandibular height							
males		26.0	0.920				
females		32.6	0.846				
total	30	34.2	0.626	27.0 - •43.5	P < 0.05	n.s.	10.0
Skull length							
males		10419	1.179				
females		97.7	0.943				
total	27	101.3	0.739	88.2 - 111.6	P < 0.01	P < 0.005	3.8
Zygomatic breadth							
males	'	72.4	0.684				
females		67.7	0.554				
total	26	70.0	0.412	64.0 - 78.8	P < 0.005	n:a. '	3.0
Mastoid **breadth**							
males		42.3	0.707				
females		41.5	0.572				
total	28	41..4	0.412	38.5 - 46.8	n.s.	u.s.	5.3
Interorbital width							
males		30.8	0.864				
females		30.6	0.673				
total	26	30.7	0.535	25.2 - 34.6	n.s.	.n.s.	8.9
Diastema (maxillary)							
males		31.1	0.702				
females		27.8	0.642				
total	26	29.4	0.443	23.7 - 38.5	P < 0.005	P <0.005-	7.7
Diastema (mandibular)							
males		18,	0.474				
females		16.7	0.515				
total	30	17.8	0.336	13.7 - 23.3	P <0.01	p <0.005	10.3
Molar axis (mandibular)							
males		29.7	0.335				
females		28.5	0.367				
total	31	29.1	0.239	22.1 - 28.8	P <0.01	n.s.	4.6
Molar axis (maxillary)							
males		25.8	0.439				
females		24.9	0.426				
total	30	25.4	0.289	26.0 - 32.3		n.s.	4.4
Length of nasals							
males		36.2	0.773				
females		36.2	0.831				
total	29	36.2	0.542	30.8 - 41.0	n.s.	n.s.	8.1
Width of nasals (front)							
males		21.8.	0.330				
females		21.7	0.356				
total	29	21.8	0.232	19.0 - 23.9	n.s.	P < 0.01	5.7
Width of nasals (rear)							
males		19.4	0.509				
females		19.2	0.547				
total	29	19.3	0.357	16.4 - 23.9	n.s.	n.s.	10.0
Skull weight							
males		70.7	3.476				
females		65.3	2.751				
total	23	67.7	1.895	51.2 - 88.9	n.s.	n.s.	13.4

length of the type male was within the range for Harding County males, but was 3.8 mm longer than the mean (36.2 mm). Western porcupines (E. d. epixanthum Brandt) have longer nasals than eastern subspecies (Anderson and Rand 1943).

One of the primary cranial characteristics distinguishing E. d bruneri from other subspecies is a pronounced posteriad narrowing of the nasals (Swenk 1916). The nasals of skulls collected in Harding County narrowed only slightly posteriorly, tapering from 21.8 to 19.3 mm (Table 10). Nasals of the E. d. bruneri type male were much more narrowed, tapering from 21 mm anteriorly to 15.5 mm posteriorly (Swenk 1916).

Differences in skull characteristics, particularly shape of nasal bones and overall size, indicate that Harding County porcupines are an intergrade between E. d. bruneri and the western yellow-haired porcupine E. d. epixanthum Brandt, which is found in North Dakota and Montana (Hall and Kelson 1959). Hall and Kelson (1959) list marginal records of E. d. bruneri from Nebraska, Oklahoma, Kansas, Texas, and Colorado, all south of South Dakota. Anderson and Rand (1943) regard the subspecies E. d. bruneri of doubtfull occurrence in Canada, if considered a tenable form. Swenk (1916) described a Montana specimen and specimens from Idaho and Utah as possible intergrades with E. d. epixanthum because the nasal bones did not narrow posteriad and they were smaller than the type specimen, the same characteristics possessed by Harding County specimens. Similarity in pelage of Harding County specimens to E. d. bruneri when skull characteristics were dissimilar may be explained by the fact that in porcupines intergradation in skull characteristics does not always occur in the same geographic area as intergradation in pelage characteristics (Anderson and Rand 1943).

SUMMARY

(1) Summer home ranges of porcupines in Harding County were larger than have been recorded in other areas. Adult females had home ranges from 61.5 to 303.4 ha (mean = 158.2 ha). Homes ranges of juveniles were from 49.9 to 130.9 ha (mean = 90.4 ha). Adult males were more sedentary; their home ranges were 49.8 to 60.4 ha (mean = 57.9 ha). Differences in summer range sizes between adult females and adult males was attributed to energetic demands of pregnancy and lactation.

(2) Daytime cover preferences were determined by telemetry. Silver buffaloberry was the most frequented cover; it also served as a year-round food source. Snowberry, a commonly used cover, gave little protection and was not eaten; its high use was attributed to its abundance. Earth dens dug by other animals were used where rock dens were not available. Porcupines seemed intolerant of heat and used dens in summer as well as winter.

(3) Food habits were determined by microscopic examination of fecal and stomach contents. Grasses were of little significance, although occasional samples had a high percentage of grass. Crested wheatgrass was the most common grass eaten. Forbs were eaten all seasons. Alfalfa was the most frequently consumed forb, followed

by wild licorice, yellow sweetclover, bigtop dalea, narrowleaf goldenaster, and sages. Haystacks, which procupines used as winter dens, were a source of alfalfa and yellow sweetclover during the winter. Locoweed was eaten with no apparent ill effects. Shrubs formed the major portion of the diet from May through October and in late winter. The most frequently consumed species was buffaloberry, followed by fruits of several species, then hawthorne and skunkbrush. Five species of trees were identified in the diet. Ponderosa pine was the most frequently eaten, although the quantity was often small. Thirty-eight percent of all samples contained willow; it was often a large part of the meal. Green ash was eaten by 20 percent of the individuals. Large quantities were not eaten, and because it was the most common tree in prairie draws, it was probably not palatible. Where willow or poplar were abundant ash was not utilized.

The digestibility of pine inner bark is 83.6 percent, and of alfalfa, 77.6 percent. The amount of forage digested (6.7 g/kg per day) was the same on both rations. This amount did not meet the energy needs of porcupines and weight loss occurred. Pine inner bark was too low in protein to meet the nutritional needs of porcupines.

(4) Of 174 porcupines captured in Harding County, 120 were adults and 54 were young-of-the-year. The population was 34 percent adult males, 16 percent juvenile males, 34 percent adult females, and 15 percent juvenile females. The apparent sex ratio changed with season, due to changes in behavior associated with reproduction.

Among males, older age-groups became reproductively active earlier in the season than younger ones. The population in Harding County was young; only four percent of the population were four years of age or older. Thirty-three percent were young-of-the-year, 14 percent were one year old, and 49 percent were two or three years old. The lack of older age-classes indicated high adult mortality rates. Reproduction rates were high, 54 young per 60 adult females. Most of the mortality in telemetry animals was related to man. An increase in human population in Harding County, which is likely because of recent energy development, would place the porcupine population under stress. Porcupines are highly visible on the prairie, and are an easy target for varmint hunters. Planting of alfalfa along roads as a hay crop attracts the porcupines to roadsides and causes increased traffic kills.

(5) The metabolic rates of adult porcupines in thermoneutrality, increase in metabolic rate with increased temperature, and the metabolic rate of a juvenile were determined by oxygen consumption. The mean resting metabolic rate of adult porcupines was 64.67 $W_{(kg)}^{0.77}$ kcal/day. There was no difference in metabolic rate between sexes or between the lactating female and non-lactating females. The metabolic rate of a one-week-old juvenile was nearly double the resting metabolic rate of adults. Growth rates of juvenile porcupines, low compared to other rodents, were highest in the first week of life (IGR = 0.039 to 0.059/day). Increased nutrition increased growth rates by 30 percent.

Rises in metabolic rates with ambient temperature followed the regression equation Y = 15.24 + 1.15 X, where Y is metabolic rate in kcal • kg^{-1} day^{-1} and X is ambient temperature above 23 C. Porcupines were intolerant of heat; body temperatures rose rapidly and animals became prostrate above 35 C. In a hot climate protection from heat in summer may be more essential to porcupine survivial than protection from cold in winter.

(6) External parasites of Harding County porcupines were lice (Trichodectes setosus), ticks (Dermacentor andersoni), and fleas (Arctopsylla setosa). A. setosa is a carnivore flea, and has not previously been found in South Dakota or on a rodent host.

(7) Porcupines in Harding County appeared to be an intergrade between two subspecies, E. dorsatum bruneri Swenk and E. d. epixanthum Brandt. Coloration resembled E. dorsatum bruneri, but the nasal bones did not narrow posteriad and the animals were smaller than the type E. d. bruneri. E. d. epixanthum is found in Montana and North Dakota, and is similar to Harding County specimens in nasal bone characteristics and body size.

REFERENCES CITED

Anderson, R. M. and A. L. Rand. 1943. Variation in the porcupine (Genus _Erethizon)_ in Canada. Can. J. Res. 21(9):292-309.

Baudenette, R. V. 1972. Energy metabolism and evaporative water loss in the California ground squirrel. J. Comp. Physiol. 81(1):57-72.

Brander, R. B. 1971. Longevity of wild porcupines. J. Mammal. 52(4):835.

Brody, S. 1945. Bioenergetics and growth. Hafner Press, New York. 1023pp.

California Department of Fish and Game. 1962. Job Completion Report, Investigation Project W-52-R-6. Wildlife Investigations Laboratory, Job No. 4: Miscellaneous Food Habits Studies, July 1, 1961 to June 30, 1962. Unpbl. Rpt.

Chew, R. M. 1960. Porcupines in the Chiricahua Mountains, southeastern Arizona. J. Mammal. 41(1):132-133.

Cockrum, E. L. 1954. Non-geographic variation in cranial measurements of wild-taken _Peromyscus leucopus noveboracensis._ J. Mammal. 35(3):367-376.

Cook, W. C. 1972. Comparative nutritive values of forbs, grasses and shrubs. Pages 303-310 in C. M. McKell, J. P. Blaisdell, and J. R. Goodin, eds. Wildland shrubs - their biology and utilization. USDA For. Serv. Gen. Tech. Rpt. INT-1. Intermountain Forest and Range Exp. Stn., Ogden Utah.

Curtis, J. D. and E. L. Kozicky. 1944. Observations on the eastern porcupine. J. Mammal. 25(2):137-146.

Dietz, D. R. 1972. Nutritive value of shrubs. Pages 289-302 in C. M. McKell, J. P. Blaisdell, and J. R. Goodin, eds. Wildland shrubs - their biology and utilization. USDA For. Serv. Gen. Tech. Rpt. INT-1. Intermountain Forest and Range Exp. Stn., Ogden Utah.

Dodge, W. E. 1967. The biology and life history of the porcupine (Erethizon dorsatum) in western Massachusetts. Ph.D. thesis, Univ. of Massachusetts (Libr. Congr. Card No. Mic. 68-3409). University Microfilms. Ann Arbor, Mich. 162pp.

Fracker, S. B. and J. A. Brischle. 1944. Measuring the local distribution of Ribes. Ecology 25(3):283-303. (As reported in Hanson, 1971).

Hall, E. R. and K. R. Kelson. 1959. The mammals of North America. Ronald Press Co., New York. Vol. 2, 547-1083pp.

Hanson, R. M. 1971. Drawings of tissues of plants found in animal diets and in the litter of grasslands. U. S. Int. Biol. Grasslands Biome Tech. Rep. 70. Colorado State Univ., Fort Collins. 14pp.

Hibbard, C. W. 1934. The occurrence of E. epixanthum bruneri and Mustela nigripes in Kansas. J. Mammal. 15(1):70-71.

Horwitz, W. ed. 1975. Official methods of analysis. Association of Official Agricultural Chemists 12th ed. Washington, D.C. 757pp.

Irving, L., and H. Krog. 1954. The body temperature of arctic and subarctic birds and mammals. Jour. Appl. Physiol. 6(11):667-680.

, and M. Monson. 1955. The metabolism of some Alaskan animals in winter and summer. Physiol. Zool. 28(3):173-185.

Johnson, D. R. and K. L. Groepper. 1970. Bioenergetics of north plains rodents. Am. Midl. Nat. 84(2):537-548.

Johnson, J. R. and J. T. Nichols. 1970. Plants of South Dakota grasslands. Bull. 577, Agric. Exp. Stn., South Dakota State University, Brookings. 163pp.

Johnson, J. L. and R. H. McBee. 1967. The porcupine cecal fermentation. J. Nutr. 91:540-546.

Kamstra, L. 1975. Nutrition of farm animals. Kendall/Hunt Publishing Co., Dubuque, Iowa. 207pp.

Kelley, G. M. 1970. The biology of an isolated porcupine population. M.S. Thesis, Univ. of Massachusetts. 48pp.

Kleiber, M. 1961. The fire of life. John Wiley & Sons, Inc. New York. 545pp.

Krefting, L. W., J. H. Stoekler, B. J. Bradle, and W. D. Fitzwater. 1962. Porcupine-timber relationships in the lake states. J. For. 60(5):325-330.

McNab, B. K. 1963. Bioenergetics and the determination of home range size. Amer. Nat. 97(894):133-140.

Marshall, W. H., G. W. Gullion and R. G. Schwab. 1962. Early summer activities of porcupines as determined by radio-positioning techniques. J. Wildl. Manage. 26(1):75-79.

Morhardt, S. S. and D. M. Gates. 1974. Energy-exchange analysis of the belding ground squirrel and its habitat. Ecol. Plonogr. 44(1):17-44.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. Am. Midl. Nat. 37(1):223-249.

Monson, G. 1948. Porcupines in southwestern Arizona. J. Mammal. 29(2):182.

Prosser, C. L. 1973. Comparative animal physiology. 3rd ed. W. B. Saunders Co. Philadelphia, London, and Toronto. 966pp.

Pulich, W. M. 1953. Some porcupine records for the Colorado River, Nevada. J. Mammal. 34(2):259-260.

Reynolds, H. G. 1957. Porcupine behavior in the desert-shrub type of Arizona. J. Mammal. 38(3):418-419.

Shadle, A. R. 1951. Laboratory copulations and gestations of porcupine, Erethizon dorsatum. J. Mammal. 32(2):219-221.

Smith, G. W. 1975. An ecological study of the porcupine (Erethizon dorsatum) in the Umatilla National Forest, northeastern Oregon. M.S. thesis, Washington State University. 101pp.

Soholt, L. F. 1973. Consumption of primary production by a population of kangaroo rats (Dipodomys merriami) in the Mojave Desert. Ecol. Monogr. 43(3):357-376.

Sphuler, W., W. F. Lytle, and D. Moe. 1971. Climate of South Dakota. South Dakota State Univ., Agric. Exp. Stn. Bull. 582. 30pp.

Spencer, D. A. 1946. A forest mammal moves to the farm - the porcupine. Trans. N. Am. Wildl. Conf. 11:195-199.

Steel, R. G. and J. H. Torrie. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc. New York. 481pp.

Swenk, M. H. 1916. On a new subspecies of porcupine from Nebraska. Univ. Nebraska Studies 16(1/2):115-125.

Taylor, W. P. 1935. Ecology and life history of the porcupine (*Erethizon epixanthum*) as related to the forests of Arizona and the southwestern United States. Univ. Arizona Bull. 6(5):1-177.

Ullrey, D. E., W. G. Youatt, H. E. Johnson, L. D. Fay, and B. E. Brent. 1967. Digestibility of cedar and jack pine browse for the white-tailed deer. J. Wildl. Manage. 31(3):448-454.

Van Bruggen, T. 1976. The vascular plants of South Dakota. Iowa Univ. Press, Ames. 538pp.

Westin, F. C., G. L. Buntley, and L. F. Puhr. 1967. Soils of South Dakota. South Dakota State Univ. Agric. Exp. Stn. Soil Surv. Ser. No. 3. 32pp.