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FACTORS AFFECTING SELECTION OF WINTER FOOD AND ROOSTING RESOURCES BY PORCUPINES IN UTAH

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ABSTRACT.—Ecological and phytochemical factors potentially affecting winter dietary discrimination by porcupines (*Erethizon dorsatum*) in the mountain brush zone of Utah were studied. Porcupines utilized gambel oak (*Quercus gambelii*) as their primary winter food and roosting resource. Big-tooth maple (*Acer grandidentatum*) was the most common tree species in the study area but was rarely utilized by porcupines. Conifer species were used as a food and roosting resource significantly less often than they occurred in the study area, despite thermal advantages provided by their relatively dense canopies. Oak feed trees were successfully separated from conifer feed trees by discriminant analysis 100% of the time. Oak trees were correctly classified as feed and nonfeed trees 71% of the time. Gambel oak contained higher amounts of crude protein, fiber, and tannins, but was lower in ether extract fractions and fatty acid content than conifers. A layer of adipose tissue used as an energy reserve by porcupines may have relaxed energy intake demands sufficiently to permit them to concentrate on a diet of oak tissue, which is high in protein, rather than a high-fat conifer diet. A diet relatively high in protein may have facilitated digestion of food material high in fiber. Temperature did not affect selection of tree species used for roosting. Rock and snow caves were utilized infrequently and the study population ranged widely. Three of 15 study animals were eaten by predators.

Key words: porcupine, Erethizon dorsatum, *gambel oak,* Quercus gambelii, *dietary selection, mountain brush zone, predation.*

Porcupines (*Erethizon dorsatum*) roost and feed in canopies of deciduous trees and shrubs for extended periods during winter in much of western North America (Oveson 1983, Craig and Keller 1986, Sweitzer and Berger 1992). Apparent localized interspecific and intraspecific preferences for food and shelter resources by porcupines imply that chemical and/or physical advantages are available to them. Further, since snow caves, rock dens, and cover in canopies of coniferous tree species likely offer increased thermal advantages in the form of energy savings to porcupines (Clarke and Brander 1973, Roze 1987, 1989), their dependence on a deciduous food and roosting resource (which does not offer those advantages) further strengthens the implication that chemical and/or physical selective advantages are realized by dietary selection. Predator avoidance may also be an important force in food and roost tree selection. The objective of this research was to investigate physical, phytochemical, and ecological agents involved in selection of gambel oak by porcupines in south central Utah.

STUDY AREA

The study was conducted in the mountain brush zone near the mouth of Spanish Fork Canyon in north central Utah. Elevations at the study site range from 1650 to 2075 m. The general exposure is northern, and terrain is steep. Overstory woody vegetation is dominated by gambel oak (*Quercus gambelii*) and bigtooth maple (*Acer grandidentatum*). Aspen (*Populus tremuloides*), chokecherry (*Prunus virginiana*), Douglas fir (*Pseudostuga menziesii*), white fir (*Abies concolor*), and mountain maple (*Acer glabrum*) are also represented in the woody flora. The climate in Spanish Fork Canyon during the winter of 1984–85 was not atypical. Data from the Spanish Fork U.S. Climatological Station, located approximately 5.5 km from the study site, indicate that temperatures were slightly colder and precipitation was slightly higher than average (U.S. Climatological Data for Utah 1984–85). Coyote (*Canis latrans*) and mountain lion (*Felis concolor*) tracks were frequently encountered in the study area. Private access into the study area allowed observation

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of a porcupine population relatively free from human disturbance.

METHODS

Fieldwork

We conducted fieldwork from late December 1984 through April 1985, at which time the study population had shifted from a diet of inner bark (phloem and cambium) of woody vegetation to herbaceous vegetation. The study area was systematically searched by researchers on snowshoes. Study animals were captured by hand, usually while they were still in tree canopies. This was accomplished by grasping distal guard hairs at the posterior end of the tail between thumb and forefinger and pulling the tail taut. The captured animal was then secured by grasping the tail with the free hand using a backward stroking motion to flatten the quills. Fifteen porcupines, 10 females and 5 males, were instrumented with radio transmitter collars (Telonics, Inc.). Animals were located daily by triangulation, and visual sightings were made on each animal approximately weekly.

Percent occurrence of woody species was calculated from point-quarter measurements using the feed/roost tree as the center point (Cottam and Curtis 1956). Percent occurrence of woody species vs. percent utilization of each feed tree species was compared using chi-square analysis to test whether feed tree selection was random. Diameter at breast height (dbh), species, and distance from the feed tree center point were recorded for the nearest woody stem in each quadrant. Point-quarter measurements were repeated using the nearest neighbor nonfeed tree of the same species as the center point. Tissues from feed and nonfeed trees were collected to investigate possible differences in chemical makeup. Tissue samples from feed trees were collected where fresh bark removal indicated the roosting animal had foraged. Samples from nearest neighbor nonfeed trees were taken from branches at the same height and with a diameter similar to those from corresponding feed trees. Bark samples were frozen and analyzed for dietary components. Results from those analyses reasonably approximated values reported for gambel oak (Smith 1957, Kufeld et al. 1981, Welch 1989). Location, slope, aspect, snow depth, and climatic conditions were recorded at each feed tree site. High and low temperature readings were taken daily at an elevation of 1597 m, as well as from the Spanish Fork climatological station.

Laboratory and Statistical Methods

Tissues from feed and nonfeed trees were analyzed for protein and phosphorus using the auto analyzer semiautomated method #12 for feeds (Horwitz 1980). Calcium, magnesium, potassium, and sodium content were determined by the atomic absorption method #2 for plants (Horwitz 1980). Sulphur content was determined by a wet-ash process using nitric and perchloric acid. Crude fiber was determined by the acid detergent fiber and lignin #21 method (Horwitz 1980). An evaluation of crude fat was made using the direct method (Horwitz 1980) on a Lab Con soxlet extractor. A limited number of tissue samples were analyzed on a Hewlett Packard model 5995 gas chromatograph/mass spectrometer (GCMS) for fatty acids and terpenes. Tannin content was measured by the radial diffusion method (Hagerman 1987) with quebracho tannin being the standard, and by astringency (Gambliel et al. 1985). Soluble carbohydrates were determined according to daSilveira (1978). Urine samples of captive porcupines on a strict diet of gambel oak were analyzed for calcium and phosphorus content when laboratory results indicated the Ca/P ratio in the tissue of food materials was greater than expected. Eight oak tissue samples were chosen at random and retested for calcium and phosphorus content according to Horwitz (1980) on a Beckman DU-30 spectrophotometer.

Differences between oak, white fir, and Douglas fir feed and nonfeed trees were statistically analyzed to help discern foraging patterns used by instrumented porcupines. Chemical and ecological factors were evaluated for between-species differences using two-sample t tests, and for within-species differences with paired t tests (Minitab 1982). Statistical results are reported at the $p < .05$ and $p < .1$ levels. Chi-square analysis was used to determine if utilization of feed tree species by porcupines differed from the expected. Discriminant analysis using backward elimination and forward selection (SAS 1985) was used to determine chemical and ecological factors that best discriminate between tree species, and between feed and nonfeed trees of the same species.

TABLE 1. Mean values for factors tested for possible effects on porcupine herbivory.

	Oak (1)		White fir (2)		Douglas fir (3)	
	Nonfeed tree **$n = 46$	Feed tree $n = 46$	Nonfeed tree $n = 3$	Feed tree $n = 3$	Nonfeed tree $n = 7$	Feed tree $n = 7$
Distance from conifer (m)	—	207	—	0	—	0
Distance to feed tree, same sp. (m)	—	358^{2}	—	543^{1}	—	377
Wind speed (mph)	—	5.5^{3}	—	3.7	—	9.7^{1}
Slope (%)	—	33.5^{3}	—	36.5	—	42.4^{1}
Elevation (m)	—	1779^{2}	—	$1937^{1,3}$	—	1680^{2}
Dbh (cm)	*13.2	$16.5^{2,3}$	*25.4	40.4^{1}	33.3	34.5^{1}
Crude fiber (%)	43.3	44.2^{3}	43.6	48.0^{3}	42.4	$40.1^{1,2}$
Protein (%)	4.9	$5.0^{2,3}$	4.0	4.2^{1}	4.0	3.9^{1}
Phosphorus (%)	0.038	0.039	0.087	0.064	0.038	0.042
Ether extract fractions (%)	9.0	$9.1^{2,3}$	15.7	$12.7^{1,3}$	16.5	$18.9^{1,2}$
Water	41.0	$39.6^{2,3}$	46.1	49.7^{1}	53.4	50.7^{1}
Potassium (%)	0.39	0.39^{3}	0.36	0.31	0.16	0.19^{1}
Calcium (%)	2.7	2.7^{3}	2.8	2.7	1.7	1.7^{1}
Magnesium (%)	0.137	$0.142^{2,3}$	0.083	$0.092^{1,3}$	0.068	$0.065^{1,2}$
Sodium (ppm)	51.1	54.0	53.7	60.0	71.6	58.0
Sulfur (%)	0.20	0.19	0.70	0.48	0.14	0.35
pH	4.7	4.7^{3}	4.7	4.7^{3}	4.3	$4.4^{1,2}$
Tannins (radius in cm)	30.5	$29.6^{2,3}$	17.5	$17.9^{1,3}$	26.2	$25.0^{2,3}$
***Astringency (mg/g fw)	85.8	83.0	*48.7	66.3	104.3	95.8
Sodium salts (%)	2.9	3.0	3.0	3.3	2.9	3.4
Soluble carbohydrates (%)	16.02	16.20	—	—	17.33	16.58
FA (GCMS count units)	827,905	399,239	—	2,609,969	—	1,259,531

Superscript values indicate differences between species at the $p < .1$ level or less. 1 = oak, 2 = white fir, 3 = Douglas fir.

*Values different between feed and nonfeed trees of the same species at or below $p < .1$.

** Multiple locations in the same tree responsible for different n values used in calculations of chemistry and climatic data. Climatic data n values are the same as reported in Table 3.

*** Not comparable across species boundaries.

n values for factors below dashed line not as reported for rest of column. Not statistically comparable due to smaller sample size.

RESULTS

Oak and white fir feed trees were larger than nonfeed trees of the same species ($p < .05$, Table 1). Herbivory by porcupines in deciduous species occurred in the canopies of large trees or in shrubs where branch diameters were relatively small. In coniferous species herbivory was also concentrated in the canopy rather than on the tree bole. Only two instances of chipping bark off the bole to expose the inner bark were noted in our study, both on deciduous tree species. There were no trends correlating calendar date or temperature to selection of feed tree species. Douglas fir feed trees contained greater amounts of crude protein than Douglas fir nonfeed trees ($p < .05$). Crude protein content of both conifer species was less than that of oak trees (Douglas fir $p < .05$, white fir $p < .1$). Total tannins (as measured by radial diffusion) were higher in oak than in conifers (Douglas fir $p < .1$, white fir $p < .05$). Astringency (protein binding capacity) was not comparable among species but was greater for white fir feed trees than nonfeed trees ($p < .1$). Ether extract fractions were lower in oak than in conifers ($p < .05$) and lower in white fir than Douglas fir ($p < .1$).

Tissue from Douglas fir contained less crude fiber than tissue from oak and white fir ($p < .05$), and Douglas fir feed trees contained still less than nonfeed trees ($p < .1$). Water content was lower in oak tissue than in conifer tissue ($p < .05$). Oak contained higher levels of potassium and calcium than Douglas fir ($p < .05$). White fir was also higher than Douglas fir in calcium ($p < .05$). Magnesium levels for oak were greater than for either conifer species ($p < .05$). White fir and oak tissue had higher pH values than tissues from Douglas fir ($p < .05$). Oak feed trees were higher in sodium salts than Douglas fir feed trees ($p < .1$). Calcium-phosphorus ratios for feed trees were higher in oak than in Douglas fir ($p < .05$). The calcium-phosphorus ratio for oak is well above acceptable limits for mineral absorption by mammals

(Underwood 1966). High calcium-phosphorus ratios have also been reported by Masslich (1985) for aspen (*Populus tremuloides*) tissue utilized by beaver. After an independent test of feed tree tissue confirmed the high ratio, we tested the mineral content of feces and urine from captive porcupines on an oak diet. Calcium-phosphorus ratios from fecal material were 10:1, while ratios from urine were approximately 221:1.

Tissue samples from feed trees were analyzed by GCMS primarily as a check on ether extract fractions. The small sample size did not permit statistical analysis, but trends showing lower fatty acid content in oak than in conifers concurred with our observation of lower ether extract fractions in oak. The amount of fatty acids was lower in oak than in either conifer species.

Discriminant analysis correctly classified feed trees as either conifer or oak 100% of the time (Table 2). Six factors were important contributors to the model. Conifer feed trees had higher amounts of phosphorus and a greater ether extract fraction than oak feed trees. Alternatively, oak feed trees were higher in protein, calcium, tannins, and magnesium. Although tannins entered into the model, they were not a significant contributor. These differences between oak and conifer feed trees generally are in agreement with differences in Table 1. The classification of oak feed and nonfeed trees was less successful (71%, Table 2). Oak feed trees were significantly higher in sodium and fiber than nonfeed trees, while nonfeed trees were higher in water content.

Porcupines used gambel oak as a food source more often than it occurred in the study site (p values listed in Table 3). Six of 15 animals were found roosting and feeding exclusively in oak, while 9 roosted and fed in conifer species at least once. Snow depths and temperatures were analyzed for the winter period before the main snowmelt (judged to be 18 March). Average snow depths at porcupine location sites for that time period were 0.60 m. Maximum snow depth was 1.20 m (median 0.65 m). Mean minimum temperature for the night previous to locating study animals was −10°C; the extreme low was −27°C. Mean temperature for the night previous to locating animals in rock or snow caves was −12°C. There was no statistical difference between the minimum nightly temperature previous to locating porcupines in station trees compared to locating porcupines in rock or snow dens.

There were approximately 7.0 porcupines/km^2 in the study area. Radio-collared animals were far ranging and did not utilize a single den or station tree as a base from which to launch foraging expeditions. Rather, they roosted and fed in a single tree for one to several days and then moved to another roost and feeding tree. Death loss due to predation and other causes left only 3 of 5 male and 6 of 10 female porcupines instrumented with radio transmitting devices for the entire winter. This sample size made statistical analysis of home ranges unreliable. Several animals spent the winter in relatively small areas, but most had relatively large, overlapping home ranges. Male home range extremes were 6.8 and 47.5 ha. Extremes for females were 9.2 and 61.8 ha. One female's home range overlapped those of three males and at least four other females. Movements of up to 400–500 m between relocations of some of the larger, mature animals were not uncommon. Some juvenile animals had reduced home ranges and movements, which generally agrees with observations by Roze (1989). Mean distance from oak feed trees to a potential conifer feed tree was significantly less ($p < .05$) than the distance of an average move by a porcupine from an oak feed tree to any other feed tree (Table 1).

Three of 15 porcupines (20%) were eaten by predators in a 4-mo period. Tracks in the snow indicated that one porcupine was pursued, worried, and killed by two coyotes. The other two porcupines eaten by predators died late in the season on south-facing slopes bare of snow; neither the cause of death nor carnivore species could be positively determined. Carcasses of two other porcupines that died presumably of starvation and/or exposure during the course of the study were not scavenged by coyotes.

DISCUSSION

Chemical Factors

Dietary alternatives in the form of different feed tree species, with significantly different chemical makeup, were available to the study population. In winter, vegetative oils have the potential to be the most important source of energy for porcupines. Data from ether extract fractions derived from feed tree tissues indicate

TABLE 2. Standardized canonical discriminant function coefficients for factors that discriminated between oak and conifer feed trees (100% correct classification), and between oak feed trees and oak nonfeed trees (71% correct classification).

Oak (+) vs. conifer (–) feed trees $n = 56$			Oak feed (+) vs. nonfeed (–) trees $n = 46$		
	Coefficient	Prob > b		Coefficient	Prob > b
Phosphorous	–1.24	.00001	Water content	–0.62	.006
Ether extract fractions	–0.60	.0001	Sodium	+0.61	.02
Protein	+1.18	.0005	Fiber	+0.59	.001
Calcium	+0.39	.019			
Tannins	+0.29	.175			
Magnesium	+0.24	.006			

that gambel oak, the major food source of our animals, had lower values of ether extract fractions than tissues from conifers. Evaluation of fatty acids by GCMS confirmed that fatty acid content was higher in conifer tissue. Additional research on known digestible fractions is needed, but until data indicating otherwise are presented, we will operate under the premise that for porcupines conifers provide a greater source of useable fats than do oaks. Discriminant analysis was used to determine if, when all variables were taken together, there would be general support from this analysis with the *t* test. Significant differences found by these analyses comparing oak and conifer feed trees were in agreement (Tables 1, 2). Phosphorus and the ether extract fraction were higher in conifer feed trees compared to oak feed trees, and protein, calcium, tannins, and magnesium were higher in oak feed trees. Discriminant analysis was less successful in classifying feed and nonfeed trees within oak (Table 2). An important reason for this less successful classification was that the cloning nature of oak was emphasized by the point-quarter method. This method may have resulted in selecting nonfeed trees from the same clone as the feed tree. Future research should involve delineating the boundary of the clone and selecting a nonfeed tree from a clone different from the feed-tree clone.

Conifer roost sites also offer greater thermal advantages than deciduous roost sites (Clarke and Brander 1973, Roze 1989). Despite multiple options, porcupines depended heavily on an oak diet low in fats and associated thermal advantages but higher in tannins. The advantage of the oak diet may well be that it is higher in protein. High levels of crude fiber (e.g., cellulose) reduce the digestibility of crude protein in monogastrics (Glover and Duthie 1958a, 1958b). Therefore, herbivores on a high-fiber diet would be expected to maximize the intake of crude protein to compensate for a low digestibility rate. Implications of a diet high in calcium and tannins are less clear, but it is possible that porcupines may deal with high levels of calcium in their food material by concentrating calcium in the urine. Tannins function as protein binding agents (Rhoades and Cates 1976). It is now evident that some insects can circumvent tannins through a higher gut pH and the presence of surfactants (Bernays 1981, Martin and Martin 1984, Martin et al. 1985). However, pH values for the mid-caecum (6.6), and the pyloric (1.8) and esophageal (3.2) regions of the stomach of a laboratory porcupine on a diet of oak were consistent with gut pH for monogastrics of comparable size (Hume 1982).

Oveson (1983) measured subcutaneous adipose concentrations on the rump of porcupines and reported a thickness of 15.1 mm (± 2.6 mm) in early winter. By late February and early March fat reserves were virtually nonexistent. A similar phenomenon was observed by Sweitzer and Berger (1993) in Nevada, where porcupine body condition decreased significantly throughout the winter season. Those authors suggested the change in body mass was an indication that porcupines depleted energy reserves early in the winter and were stressed nutritionally during late winter. The heavy accumulation of fat serves as an energy reserve for porcupines to draw upon throughout the winter, allowing them to concentrate on a food source relatively high in crude protein. The reduced capabilities of protein digestibility associated with a high-fiber diet may have encouraged our study animals to maximize dietary protein by selecting oak.

Porcupine herbivory was generally noted on small branches. In large trees porcupines fed high in the canopy where limbs are smaller.

TABLE 3. Chi-square analysis of percent occurrence and utilization of trees by porcupines.*

	% occurrence	% used	Chi-square value	*p* value
Oak	43.5	82.1		
			3.23	0.10
Conifer	2.7	16.4		
Maple	52.1	1.5		
			52.41	0.01
Conifer	2.7	16.4		
Oak	43.5	82.1		
			59.14	0.01
Maple	52.1	1.5		

*n values differ from those reported in Table 1 due to the extended use of some feed trees by porcupines. Occupancy of the same feed tree during more than one sampling event counted as multiple utilization of oak but not double sampled for chemistry data. Df = 1.

We observed only two instances in which porcupines chipped bark of large tree boles and fed on tissue from large dbh limbs or trunks. Selection of larger feed trees by porcupines may be related to the texture of bark and ease of climbing (Roze 1989) rather than chemistry.

Deciduous Food and Roosting Resource

Roze (1989) discussed the thermal advantages of dens and/or conifer roost trees in relation to maintenance of a core body temperature. Citing Irving et al. (1955) and Clarke (1969), he indicated that the critical external temperature below which porcupines must increase their metabolic rates to maintain a core body temperature is a range between –12 and –4°C. He suggested dens are temperature-averaging devices that protect porcupines against convectional and radiational heat loss. Station trees provide thermal advantages to porcupines (Clarke and Brander 1973) and may serve as a substitute for rock caves and snow dens. However, none of these are requisite to porcupine survival. Roze (1989) noted that porcupines may spend winters in trees away from dens and that in every report the tree species have been evergreens.

Our data conflict with this observation. Porcupines throughout western North America are able to survive using a variety of deciduous species as food and roost tree resources. Despite the prominence of literature concerning dens and conifer station trees, use of a deciduous food and roosting resource without dependence on caves or snow dens is not an anomaly for porcupines. Craig and Keller's (1986) study site in southern Idaho was at an elevation of 1525–2089 m in desert shrub habitat. Animals in this study were not observed using dens during the winter or following runways in feeding areas. They remained in the tops of hawthorne (*Crataegus douglasii*) thickets or utilized other deciduous food sources throughout the winter. Sweitzer and Berger (1993) identified buffalo-berry (*Shepherdia argentea*), willow (*Salix spp.*), bitterbrush (*Purshia tridentata*), and juniper (*Juniperus osteosperma*) as primary winter food sources of porcupines in Nevada. We have also observed the extensive use of hackberry (*Celtis occidentalis*) and green ash (*Fraxinus pennsylvanica*) by porcupines as a food and roosting resource in the Sand Hills of Nebraska and the Missouri River Breaks of South Dakota. Caves and conifers (except plantation forests and eastern red cedar [*Juniperus virginiana*]) are not available in the Sand Hills (Swinehart 1989). Oveson (1983) reported that a porcupine remained virtually motionless while perched in a gambel oak tree for a 24-h period when the ambient temperature was as low as –37°C. During a 13-d period from 30 January through 11 February, when the mean low temperature was –17°C, 3 of 25 (12%) locations of our study animals were in conifers, 4 (16%) were in rock or snow caves, and 18 (72%) were in oak. Although porcupines did select trees with a larger dbh as roosting/feeding sites, they were also often found in smallish shrubs even though large trees were readily available. It is therefore difficult to link possible benefits presumed to be available to porcupines that roost in larger trees, such as protection from the elements or from predators, to the selection shown by animals in this study.

Despite the availability of snow caves, dens, and conifer species that could provide thermal advantages, the study population was heavily

dependent on gambel oak for a roosting and feeding resource. Considering that this reliance was during a season of energetic stress, it is likely that remaining motionless in the canopy of oak trees to conserve energy while exploiting a high-protein food source is an adaptive strategy.

Movements and Predation

The availability of conifer feed trees was not limiting since the average distance between locations of study animals was significantly greater than the mean distance of a move from any roost tree to a conifer roost tree (Table 1). It does not appear that spatial relationships of the various feed tree species played a role in feed tree selection by our study population. The relatively large overlapping winter home ranges of animals in this study differ from reports of other researchers. Home ranges for porcupines in northwestern Minnesota were small enough to be reported in square meters (Tenneson and Oring 1985). Curtis (1941), Dodge (1967), Brander (1973), Roze (1987, 1989), and others have documented that porcupines move short distances from dens to feed trees, sometimes along permanent trails in the snow. Craig and Keller (1986) and Smith (1979) also reported reduced ranges in the winter. However, Dodge and Barnes (1975) did not indicate a similar restriction in winter movements. Roze (1987) suggested the reason may be crusted snows that bear the weight of the animals. Porcupines in our study did adeptly toboggan on crusted snows down extreme slopes in an attempt to avoid capture. However, one female moved over 450 m in fresh snow. Trails in powdery snow were often direct and suggested that a destination may have been predetermined.

Common use of oak and conifer feed trees by different porcupines occurred several times during the study, sometimes concurrently. Hedging in the canopies of gambel oak trees indicated that some trees were used consistently over time by porcupines while others were not. Consistent foraging in common trees over time may indicate a learned behavior such as that described by Glander (1981) for howler monkeys, but we hesitate to attribute it to such because porcupine young-of-the-year were usually separated from their mothers during the winter. It is possible that some young accompanied their mothers for limited periods in the winter or that more subtle cues were used to transfer the information.

Long movements between feed trees in dense oak cover by some study animals suggest that predator-prey relationships may have influenced movements. Sweitzer and Berger (1992) found that habitat use was related to the age or size class of porcupines, presumably in response to increased risk of predation to smaller porcupines. Our observations generally agree with their findings. Mountain lion and coyote tracks were seen regularly in the study area. Both species are known to prey on porcupines (Keller 1935, Robinette et al. 1959, Toweill and Meslow 1977, Maser and Rohweder 1983). The strong urine scent at station trees or dens makes porcupines readily detectable. Mountain lions are capable of knocking porcupines from the canopies of trees (Taylor 1935). If long moves decreased the predictability of mountain lions locating porcupines in station trees, it would be an adaptive strategy. However, long moves expose porcupines to terrestrial predation by mountain lions, coyotes, and wolves (*Canis lupis*, which are now extirpated from the study area) and would presumably be nonadaptive. Since ample forage exists throughout the study site and long moves to locate food resources do not appear to be a dietary necessity, long movements may be an adaptive strategy to avoid arboreal predation by mountain lions. This hypothesis deserves further examination.

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