The Canadian Field-Naturalist

Volume 119, Number 2 April–June 2005

The Influence of Thermal Protection on Winter Den Selection by Porcupines, *Erethizon dorsatum,* in Second-Growth Conifer Forests

TODD N. ZIMMERLING

Gartner Lee Limited, Suite N195, 3015-5th Avenue NE, Calgary, Alberta T2A 6T2 Canada

Zimmerling, Todd N. 2005. The influence of thermal protection on winter den site selection by Porcupines, *Erethizon dorsatum,* in second-growth conifer forests. Canadian Field-Naturalist 119(2): 159-163.

I investigated den type selection by Porcupines (*Erethizon dorsatum*), in relation to the thermal cover provided by the den type, over a period of four winters. Porcupines used log dens, stump dens and rock dens in proportion to the thermal cover provided by each den type. Based on behavioural observations of Porcupines, I assumed that the lower critical temperature for porcupines in my study area was -4ºC. Both stump and rock dens provided adequate thermal protection, under most ambient conditions, to allow Porcupines to maintain their body temperature, without increasing basal metabolic rate. In most cases rock and stump dens maintained den temperatures above -4ºC until ambient temperatures reached -12ºC or lower. In contrast log dens provided poor thermal protection, even in years of thick snowcover. When ambient temperatures dropped below -4ºC, den temperatures within log dens were also recorded below -4ºC. Log dens were used least often by Porcupines, whereas stump and rock dens were used most often. Despite the large number of potential dens available to Porcupines within the study area, den use was generally limited to three dens per porcupine per winter. The limited use of dens by an individual porcupine during winter may be related to the energetic cost of finding a new den or it may be related to specific selection criteria used by Porcupines.

Key Words: Porcupines, *Erethizon dorsatum,* winter, lower critical temperature, temperature differential, winter den, den selection, den sharing, thermal cover, thermal protection, British Columbia.

Cold temperatures can have dramatic impacts on mammals, including increasing individual mass loss and mortality rates (Moore and Kennedy 1985; Saether and Graven 1988; Sweitzer and Berger 1993). Despite the extreme cold weather conditions that may be encountered throughout the northern portions of the Porcupine's (*Erethizon dorsatum*) range, the Porcupine appears to be poorly adapted for survival in colder climates. Its dorsal pelage is sparse in comparison to other northern furbearers, and the soles of its feet are hairless and large (Folk 1966). Under winter conditions the lower critical temperature (ambient temperature at which the Porcupine must increase its basal metabolic rate above resting rate to maintain body temperature) for Porcupines is estimated to be between -12ºC (Irving et al. 1955) and -4ºC (Clarke 1969), which is high compared to other mammals living in northern climates (Scholander et al. 1950a, 1950b; Irving et al. 1955).

Given that Porcupines have a high, lower critical temperature, cold ambient temperatures must constitute a major energy cost for them. To survive in cold temperature conditions the Porcupine has evolved a number of physiological and behavioural adaptations (Clarke and Brander 1973; Roze 1987; DeMatteo and Harlow 1997). One of the behavioural adaptations is the use of a winter den. Sweitzer and Berger (1993) and Roze (1989) found that Porcupines alter their foraging patterns in response to cold weather and spend more time in dens. Radiometric measurements (Clarke and Brander 1973) indicate that cover above the back of a Porcupine, such as a conifer branch, reduces radiative heat loss, and presumably a winter den (not measured in the Clarke and Brander study) provides even greater thermal protection than a conifer branch.

The objective of this study was to determine the relative thermal protection provided to a Porcupine by different den structures and to examine whether Porcupines choose den types with respect to the thermal protection provided. Den switching and den sharing by Porcupines was also examined to compare winter denning behaviour of this study population with those from other areas.

Study Area

This study took place near Terrace, British Columbia, Canada (54°35', 12°42') in the Shames Valley (approximately 30 km west of Terrace; Figure 1). The study site was composed of three second-growth stands, (20-25 years old) located in the Coastal Western Hem-

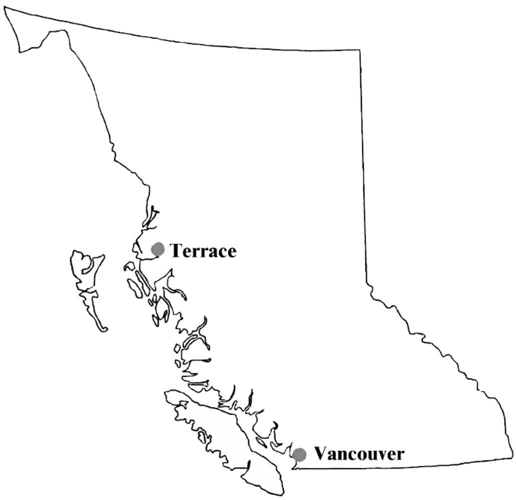

FIGURE 1: Study site location within British Columbia, Canada.

lock, wet submaritime (CWH_{ws}) biogeoclimatic subzone (Banner et al. 1993). The second-growth forest consisted primarily of Western Hemlock (*Tsuga heterophylla*), Amabilis Fir (*Abies amabilis*), and Sitka Spruce (*Picea sitchensis*) with a minor component of Western Red Cedar (*Thuja plicata*). The study stands were located on a west-facing slope with gradient up to 40% present. The lower boundaries of the study stands were at approximately 200 m elevation and the upper boundaries were at approximately 450 m elevation.

Average minimum monthly temperatures varied considerably from month-to-month and from year-to-year over the four winters of the project. Fourteen of the 20 months of this study had average minimum temperatures of –4°C or lower and 6 of the 20 months had average minimum temperatures of –12°C or lower.

Methods

During the winters (November – March) of 1996 to 2000, using systematic searches of the study area, 33 Porcupines were located and captured. Once located, the Porcupine was netted, using a large dip-net, if the animal was out of its den. If the animal was in its den, a Tomahawk, single door live-trap (40 × 40 × 100 cm) was placed at the den entrance and left overnight. Once captured, the animal was drugged using a 10:1, ketamine (10 mg/kg): xylazine (1 mg/kg) combination. To reduce the time to recovery of smaller animals, 1 kg was subtracted from body weight when determining dosage. This procedure ensured that smaller animals, that could be processed more quickly and were more susceptible to exposure to cold temperatures, recovered more quickly than larger animals that required more processing time and were less susceptible to exposure to cold temperatures.

Throughout the winter months from 1996 to 2000 each collared animal was located three times per week, using handheld telemetry. When an animal was found in a den the location was recorded using a Trimble ProXL GPS unit with differential correction (accurate to ± 1 m), and a temperature measurement from inside and outside the den was made. The temperature was measured using a Barigo digital indoor/outdoor thermometer (accurate to ± 1°C) with a 3 m probe cable. The probe was taped to heavy electrical wiring to give stiffness and to allow manipulation into the Porcupine den. When the Porcupine could be seen within the den, the probe was placed beside (but not touching) the animal. When the animal could not be seen the probe was inserted to a maximum of 2 m. In all cases the probe was positioned so as not to be resting on the den floor. The probe was left for 10 minutes to gain a stable temperature reading. Once the den temperature had been recorded the probe was then removed and placed at the top of snowcover, in a forest opening closest to the den site, to record ambient temperature.

Although a single Porcupine may have used the same den over several weeks during the winter or during two or more winters, only a single temperature measurement was taken from each den site over the course of this study. In addition to the den use by collared Porcupines, den use by uncollared Porcupines was also noted (the type of den used) when discovered fortuitously. Temperatures were not recorded at these den sites unless it was confirmed (through visual observation) that the Porcupine was occupying the den at the time.

To estimate the average maximum and minimum temperature within the study area, three monitoring sites were established within the study stand. Each monitoring station had one max/min thermometer (Taylor indoor/outdoor maximum/minimum mercury thermometer) at snow level attached to the north side of a tree. These locations were visited once per week throughout the winter months and the maximum and minimum temperature for the week was recorded and averaged with the three readings. A mean monthly maximum and minimum was then calculated for each winter month using the weekly readings.

Statistical Analysis

I compared the thermal protection provided by each den type using a single factor analysis of variance of the temperature differentials for each den type. Where required a Tukey test was used to determine which means were different (Zar 1974). Temperature differentials were calculated by subtracting the ambient temperature from the den temperature to give a positive number. When den temperatures were lower than ambient temperatures the differential was negative.

Results

Porcupines within the Shames Valley study area used four distinct den types: (1) log dens, which were defined as dens within fallen, hollow logs or dens located under a fallen tree (usually having been created by trees that had been cut down during commercial harvesting, but left on-site). (2) Stump dens, which were defined as dens located beneath the stump of a previously harvested tree. In all cases these dens were located in the rootwad of the stump, and not in any kind of hole within the stump itself. (3) Rock dens, which were dens located within the crevices of rock outcroppings. These dens were usually very deep and often had multiple, potential entrances. (4) Pre-excavated dens, which were rare in the study area, consisted exclusively of dens excavated by Coyotes (*Canis latrans*) into soft soils on gully slopes.

A total of 46 dens were measured to determine the temperature differential between den and ambient temperatures. Unfortunately, owing to the low number of pre-excavated dens used, no measurements for this den type were obtained. Rock and stump dens provided almost identical thermal protection, with mean temperature differentials of +5.4°C and +5.2 °C, respectively (Figure 2). Log dens provided the poorest insulation for Porcupines, as the best temperature differential recorded for a log den was +4°C and the mean was +1.3°C (Figure 2). This compares with the best temperature differential for a rock den of +9°C and a stump den of +10°C. Analysis of variance, with the associated Tukey test, showed log dens provide significantly less thermal protection than both rock and stump dens (ANOVA $p = 4 \times 10^{-4}$; d.f. = 2, 43; F = 9.42).

In the single case where a log den was measured while ambient temperature was below -12°C, the den temperature was also below -12°C (-16°C ambient, -15.3°C den). In nine cases where den temperatures were recorded in stump and rock dens while ambient temperatures ranged from -12°C to -20°C, the den temperatures remained above -12°C.

Of 24 observations of Porcupines out of their dens during the day, only one occurred when the ambient temperature was below -4°C (temperature was -5°C). This observation involved a Porcupine moving down a tree and travelling to a stump den, which it entered. All other observations of active animals involved Porcupines feeding or resting in trees when temperatures were between -2°C and +6°C.

If -4°C is the lower critical temperature for Porcupines, then log den temperatures were at or below the lower critical temperature in all eight cases where ambient temperature was below -4°C. Rock den temperatures were at or below -4°C in four out of twelve cases where ambient temperature was below -4°C, and stump den temperatures were at or below -4°C when ambient temperatures were below -4°C in four out of fifteen instances. In the cases where stump and rock den temperatures were below -4°C, the ambient temperature was -12°C or colder and the level of thermal protection provided by the den was high (+6.7°C to +10.0°C temperature differential).

The use of pre-excavated and log dens was similar from year-to-year, with pre-excavated dens being used in only one year (1996-1997) and log dens being used infrequently in all years (Table 1). In three of the four years the majority of dens used were stump and rock dens, the two den types with the best temperature differentials. The biggest single change in den use, from year-to-year was in the use of stump dens in 1997-1998. During this winter, the use of stump dens dropped to the lowest usage of the study (13.8%), while the use of rock dens increased to the highest usage (69.0%) (Table 1). The winter of 1997-1998, based on average weekly temperatures, was the warmest winter of the four-year study (Table 2). January was the only month in which 1997-1998 did not have the warmest maximum and minimum average temperatures, compared to the three other study years.

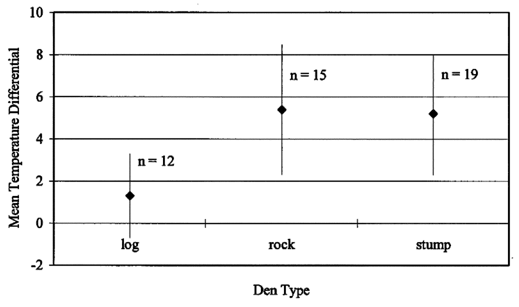

FIGURE 2: Mean temperature differential (den temperature – ambient temperature in °C) (± 1 s.d.) of winter den types used by Porcupines in the Shames Valley (All data from 1996 to 2000 combined).

The number of dens used by a single Porcupine in one winter was constant over three winters of the study. In 1996-1997, 1998-1999 and 1999-2000 individual Porcupines used an average of 3.4 dens/Porcupine, 3.3 dens/Porcupine and 3.3 dens/Porcupine, respectively. The average number of dens used by a Porcupine dropped in 1997-1998 to 2.1.

Throughout the four winters of this study individual Porcupines did not always use the same den sites from year-to-year. In some cases new dens were used every winter and in a small number of instances the same den was used by different Porcupines in two different years. Only one instance of two Porcupines using the same den at the same time was noted. This den sharing occurred in the winter of 1998-1999 and involved an adult female and a juvenile female. It was unknown if the two animals were related, but they shared the same den for 22 days without any indication of disputes occurring within the den (no sounds when den was observed by researchers).

Discussion

Porcupines in this study used four distinct den types (log, stump, rock or previously excavated dens); however, previously excavated dens were only used to a minor degree during a single winter. Unlike the results reported by Roze (1987), Griesemer et al. (1994), and Griesemer et al. (1996) all animals in this study used

TABLE 1: Winter den type selection by Porcupines in the Shames Valley (1996–2000).

Winter	n	Den Type			
		Log	Stump	Rock	Pre-excavated
1996-1997	47	17.0%	38.3%	38.3%	6.4%
1997-1998	29	17.2%	13.8%	69.0%	0.0%
1998-1999	24	12.5%	50.0%	37.5%	0.0%
1999-2000	23	17.4%	52.2%	30.4%	0.0%
Total	123	16.3%	37.4%	43.9%	2.4%

dens extensively throughout the winter and although roosting in trees during the day was noted, none spent more than a day in the shelter of conifer trees rather than in a den.

The relative use of the three common den types mirrored closely the temperature differentials found between them. Rock and stump dens had the largest temperature differentials and were used equally often through most of the study. An exception to this was the winter of 1997-1998, when rock dens were used more than in any other year and stump dens were used less often. This winter was also the warmest winter of the study. The warmer average temperature resulted in more mid-winter snowmelt than in other study years, and this may have influenced den choice by Porcupines. Stump dens tend to be low-lying and are susceptible to water seepage. As a result, increased snowmelt may have resulted in water in the den and thus lower use by Porcupines.

Log dens had the poorest temperature differential and were used least often among the three common den types. Even in years of increased snowfall, when the thick snowpack would be expected to provide increased thermal cover to a log, Porcupines did not increase the use of this den type. In all years, when ambient temperatures dropped below -4°C, log dens did not provide adequate thermal protection to Porcupines.

Roze (1989) found similar results in den use by Porcupines in the Catskill Mountains of New York State. Rock crevices were the most used denning structure (70% of dens) and hollow logs were least often used (< 10% of dens). A key difference between the Porcupines in the Catskill Mountains and the Porcupines in the Shames Valley is the use of stump dens and standing, hollow trees. In the study area chosen by Roze (1989), Porcupines used standing trees with hollow openings for dens 20% of the time, and never used stump dens, as seen in my study. The difference in den use is related to forest structure. My study site is a second-growth forest, 20–25 years of age, and, as a result, there are no trees within the study area that are old enough to have developed hollow openings in the stem. The high use of stump dens is related to previous logging activities. The removal of the large old-growth trees resulted in large stumps being left behind. As the root structure of these stumps begins to decay a natural opening is created beneath the stump in the root wad. Although Roze's study area encompassed an abandoned farm, he mentions no evidence of recent (in the last 30 years) logging on the site. As a result, stumps would only be created through natural mortality of trees. Speer and Dilworth (1978) also reported that the majority of den sites in their New Brunswick study site were located in the roots of trees. These dens, however, were not under stumps, but located in the roots of wind-thrown trees. Only one of 69 dens was located in a standing, hollow tree.

Based on behavioural observations of Porcupines during my study, I assumed that the lower critical temperature for Porcupines in the study area is closer to –4°C as reported by Clarke (1969), rather than the –12°C reported by Irving et al. (1955). In my study area, under most winter temperature conditions, Porcupines are able to rely solely on the thermal cover provided by a rock or stump den to reduce the energy requirements for maintaining body temperature, as den temperatures are maintained above -4°C. When ambient temperatures drop below –12°C, it appears Porcupines are forced to increase their metabolic rate to maintain body temperature within rock and stump dens, however, on average, temperatures within the study area were above –12°C.

Porcupines in my study were usually solitary in their den occupancy, but there was one instance where two Porcupines used the same den at the same time. The sharing of dens by Porcupines has been reported by Roze (1987), who found 12% of dens to be occupied by two Porcupines (usually a male-female pair). Dodge (1967) also described den sharing by Porcupines in western Massachusetts. In contrast, Dodge and Barnes (1975), Brander (1973) and Shapiro (1949) found that Porcupines rarely shared dens in their studies. The occurrence of winter den sharing appears to be directly correlated with the abundance of den sites in a particular area. All three studies where Porcupines were found to rarely share dens were described as having an abundance of den sites, whereas Roze (1987) describes both his study site and that of Dodge (1967) as having limited den sites. Griesemer et al. (1996) when comparing den sharing in two areas with different den availability in Massachusetts found that availability of den sites did influence den sharing by Porcupines. The results from my study also support this argument as the Shames Valley has a large number of potential den sites (as indicated by numerous unoccupied, but previously used dens).

Despite the large number of available dens, Porcupines in the Shames Valley used only a few dens per individual during a single winter (approximately three dens/Porcupine during 1996-1997, 1998-1999, and 1999-2000). In the warm winter of 1997-1998 the average number of dens used per Porcupine dropped to two. Increased snowmelt in this year may have reduced the number of dens available to Porcupines, owing to water seeping into den sites. Alternatively, the warmer temperatures may have also increased the energetic cost of travel for Porcupines by creating a soft snowpack, thereby restricting Porcupine movements. Roze (1989) reported a similar impact, with high snowfall events reducing Porcupine winter movements and numbers of dens used.

Porcupines choose den structures in relation to the relative thermal cover provided by the structure. In the case of the Shames Valley, Porcupines are taking advantage of an abundance of stump dens, which have been created as a result of past commercial forest harvesting in the area. Given the role of the winter den in Porcupine winter ecology (Roze 1987, 1989; Griesemer et al. 1994; Zimmerling and Croft 2001) it is likely that the creation of dens with high thermal cover is increasing the areas over which Porcupines can maintain winter ranges. Without the past forest harvesting Porcupines in the Shames Valley would have been limited to rock dens. Consequently Porcupine den locations would be more confined to steep areas where rock has been exposed. With the past forest harvesting activities Porcupines can find dens with good thermal cover throughout the second-growth stand and can establish winter ranges accordingly.

Acknowledgments

This research was supported financially by Skeena Cellulose Inc., Terrace Operations, and the British Columbia Ministry of Forests, Kalum Forest District. Major funding was supplied by Forest Renewal British Columbia.

I thank M. D. Bahr, M. A. Bahr, A. Coosemans, W. Croft, C. Croft, M. Dawson, B. Delahanty, M. Hamilton, C. Jardine, K. Kranrod, P. Kranrod, M. Krisinger, J. Pylon, W. Sheridan, P. Skinner, L. Zimmerling, and R. Zimmerling for their hard work under extreme field conditions. Thanks to L. Zimmerling and C. J. Krebs for reviewing an earlier draft.

Literature Cited

Banner, A., W. Mackenzie, S. Haeussleir, S. Thomson, J. Pojar, and **R. Trowbridge.** 1993. A field guide to site identification and interpretation for the Prince Rupert Forest Region. Published by Research Branch, Ministry of Forests, Victoria, British Columbia.

Brander, R. B. 1973. Life-history notes on the porcupine in a hardwood-hemlock forest in upper Michigan. Michigan Academician 5: 425-433.

Clarke, S. H. 1969. Thermoregulatory responses of the porcupine, *Erethizon dorsatum*, at low environmental temperatures. Special Report, Department of Forestry. and Wildlife Management, University of Massachusetts.

Clarke, S. H., and **R. B. Brander.** 1973. Radiometric determination of porcupine surface temperatures under two conditions of overhead cover. Physiological Ecology 46: 230-237.

DeMatteo, K. E., and **H. J. Harlow.** 1997. Thermoregulatory reponses of the North American porcupine (*Erethizon dorsatum bruneri*) to decreased ambient temperature and increased wind speed. Comparative Biochemical Physiology 116B: 339–346.

Dodge, W. E. 1967. The biology and life history of the porcupine (*Erethizon dorsatum*) in western Massachusetts. Ph.D. thesis, University of Massachusetts, Amherst.

Dodge, W. E., and **V. G. Barnes.** 1975. Movements, home-range and control of porcupines in western Washington. U.S. Depart. Fish and Wildlife Service, Wildlife Leaflet (507).

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

Griesemer, S. J., R. M. DeGraaf, and **T. K. Fuller.** 1994. Effects of excluding porcupines from established winter feeding trees in central Massachusetts. Northeast Wildlife 51: 29-33.

Griesemer, S. J., T. K. Fuller, and **R. M. DeGraaf.** 1996. Denning patterns of porcupines, *Erethizon dorsatum*. Canadian Field-Naturalist 110: 634–637.

Irving, L., H. Krog, and **M. Monson.** 1955. The metabolism of some Alaskan animals in winter and summer. Physiological Zoology 18: 173-185.

Moore, D. W., and **M. L. Kennedy.** 1985. Weight changes and population structure of raccoons in western Tennessee. Journal of Wildlife Management 49: 906-909.

Roze, U. 1987. Denning and winter range of the porcupine. Canadian Journal of Zoology 65: 981-986.

Roze, U. 1989. The North American Porcupine. *Edited by* L. Atherton. Smithsonian Institution Press, Washington, D.C.

Saether, B., and **A. J. Graven.** 1988. Annual variation in winter body condition of Norwegian moose calves. Journal of Wildlife Management 52: 333-336.

Scholander, P. F., V. Walters, R. Hock, and **L. Irving.** 1950a. Body insulation of some arctic and tropical mammals and birds. Biology Bulletin 99: 225-36.

Scholander, P. F., R. Hock, V. Walters, F. Johnson, and **L. Irving.** 1950b. Heat regulation in some arctic and tropical mammals and birds. Biology Bulletin 99: 237-258.

Shapiro, J. 1949. Ecological and life history notes on the porcupine in the Adirondacks. Journal of Mammalogy 30: 247-257.

Speer, R. J., and **T. G. Dilworth.** 1978. Porcupine winter foods and utilization in central New Brunswick. Canadian Field-Naturalist 92: 271-274.

Sweitzer, R. A., and **J. Berger.** 1993. Seasonal dynamics of mass and body condition in Great Basin porcupines (*Erethizon dorsatum*). Journal of Mammalogy 74: 198-203.

Zar, J. H. 1974. Biostatistical analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, USA.

Zimmerling, T. N., and **C. D. Croft.** 2001. Resource selection by porcupines: Winter den site location and forage tree choices. Western Journal of Applied Forestry 16: 53-57.

Received 4 March 2002
Accepted 14 May 2005