

Behavioural responses of wintering porcupines to their heterogeneous thermal environment¹

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Abstract: Many species use behavioural thermoregulation to cope with changes in their thermal environment. Most studies to date, however, have focused either on ectotherms or on endotherms living in warm environments. Here we used heated taxidermic mounts to characterize microclimates available to North American porcupines during the cold Canadian winter. We then examined activity patterns and microhabitat use of wild individuals to test whether porcupines responded behaviourally to changes in thermal conditions. Dens offered good protection against the cold, and porcupines modified their use of dens as thermal conditions became more constraining. They reduced time spent outside of dens, increased the number of activity bouts in a day, and became more diurnal. When outside of dens, they fed more often, but did not change their use of microhabitats as thermal conditions became most constraining. Microhabitats other than dens were less predictable in the protection they offered against cold temperatures. This may be why porcupines based their behavioural thermoregulation strategy on modulating patterns of den use rather than on selecting warmer microclimates when outside of the den. We hypothesize that selection of microhabitats outside of the den was driven by food acquisition or predation risk.

Keywords: behavioural thermoregulation, *Erethizon dorsatum*, foraging strategy, herbivore, operative temperature.

Résumé : Beaucoup d'espèces utilisent la thermorégulation comportementale pour s'ajuster à leur environnement thermique. Cependant, la plupart des études menées jusqu'à présent concernaient soit des ectothermes, soit des endothermes vivant dans des milieux chauds. Nous avons utilisé des mannequins taxidermiques chauffés pour caractériser les microclimates disponibles aux porcs-épics d'Amérique pendant l'hiver canadien. Nous avons aussi examiné les patrons d'activité d'individus sauvages et leur utilisation des microhabitats afin de tester si les porcs-épics modifiaient leur comportement en fonction des conditions thermiques. Les tanières offraient une protection importante contre les températures froides. Les porcs-épics les utilisaient plus lorsque les conditions thermiques étaient plus contraignantes, tout en augmentant le nombre de sorties par jour et en devenant plus diurnes. À l'extérieur des tanières, les porcs-épics mangeaient plus souvent lorsque les conditions thermiques devenaient plus contraignantes, mais ne changeaient pas leur utilisation des microhabitats. Les microhabitats autres que les tanières étaient moins prévisibles quant à la protection offerte contre les températures froides. C'est probablement pourquoi les porcs-épics basaient leur stratégie de thermorégulation comportementale sur une modulation de l'utilisation des tanières, plutôt que sur une sélection des meilleurs microclimates une fois à l'extérieur. Nous suggérons que la sélection des microhabitats extérieurs était plutôt influencée par l'acquisition de nourriture ou le risque de prédation.

Mots-clés : *Erethizon dorsatum*, herbivore, recherche alimentaire, température opérante, thermorégulation comportementale.

Nomenclature: Banfield, 1974.

Introduction

Behavioural thermoregulation is an animal's primary strategy to deal with changes in the thermal environment (Satinoff, 1996). It has been documented in all types of species, from small ectothermic insects (Willmer, 1991) to large endothermic mammals (Dussault *et al.*, 2004; Maloney *et al.*, 2005). Most studies on endotherms have focused on small mammals living in hot environments (Vispo & Bakken, 1993; Sharpe & Van Horne, 1999), but endotherms in cold environments also display many thermoregulatory behaviours. They use a shelter or vary

group size to reduce heat loss (Berteaux *et al.*, 1996), vary activity patterns with temperature (Humphries *et al.*, 2005), select foraging microhabitats (Wiersma & Piersma, 1994), or use postures promoting heat conservation (Fortin & Gauthier, 2000).

Studies on behavioural thermoregulation generally focus on the alteration of activity patterns with changing air temperature at the study site. However, air temperature at a study site can be insufficient to describe the thermal environment experienced by an animal because it does not account for the influences of wind, radiative sources (the sun), and sinks (a cloudless sky) (Lustick, Battersby & Kelty, 1978; Bakken, 1991), and there are many microclimates in a given habitat (Sharpe & Van Horne, 1999). A detailed description of an animal's thermal environment is

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thus necessary to evaluate the ecological effectiveness of its thermoregulatory behaviour.

The North American porcupine (*Erethizon dorsatum*) is the only arboreal folivorous mammal of the boreal forest. It stays active year round and relies on low-quality food during winter (Roze, 1989). The lower critical temperature (the temperature below which an organism increases metabolic rate above basal to maintain its body temperature) of winter acclimatized porcupines varies between $-12\text{ }^{\circ}\text{C}$ and $+10\text{ }^{\circ}\text{C}$, depending on their size and origin (e.g., DeMatteo & Harlow, 1997; Fournier & Thomas, 1999). In southern Canada during winter, adults weigh between 5 and 10 kg (D. Berteaux, unpubl. data), their lower critical temperature lies around $-2\text{ }^{\circ}\text{C}$ (Fournier & Thomas, 1999), and they face temperatures that can be as low as $-35\text{ }^{\circ}\text{C}$. Although porcupines can den, they must feed daily in the tree canopy, which should be energetically demanding because wind speed increases with height above ground (Byman, Hay & Bakken, 1988). However, the tree canopy offers various microhabitats to a mid-sized mammal.

How porcupines use their den and select feeding microhabitats could greatly affect their thermoregulatory costs, so porcupines are good candidates to evaluate the effects of thermal conditions on thermoregulatory behaviour of wintering endotherms. We characterized the general thermal conditions prevailing at the scale of a forest stand in southern Canada, taking into account temperature, convection, and radiation (see Methods). We then used those general thermal conditions in the stand as a central variable to study

behavioural thermoregulation of free-ranging porcupines through 3 specific objectives (Figure 1).

Objective 1: Our first objective was to assess, using heated taxidermic mounts, the relative thermal quality of 6 microhabitats for the range of thermal conditions encountered through winter. Predictions: Dens are of better thermal quality than outside microhabitats when thermal conditions are most constraining, and terrestrial and covered microhabitats are of better thermal quality than arboreal and open microhabitats, respectively.

Objective 2: Our second objective was to evaluate, using movement detectors and radiotelemetry, how porcupines change their activity patterns with variations in thermal conditions. Prediction: Porcupines modify their activity patterns with thermal conditions in order to reduce exposure to cold temperatures.

Objective 3: Our third objective was to assess, using radiotelemetry, how porcupines change their use of outside microhabitats with variations in thermal conditions. Prediction: Porcupines select microhabitats of better thermal quality when thermal conditions are most constraining.

Methods

STUDY AREA AND STUDY POPULATION

We worked during 2 winters (2004 and 2005) in a 2-km² area of parc national du Bic ($48^{\circ} 20' \text{ N}$, $68^{\circ} 46' \text{ W}$, elevation 0–150 m), Quebec, Canada. The study area is

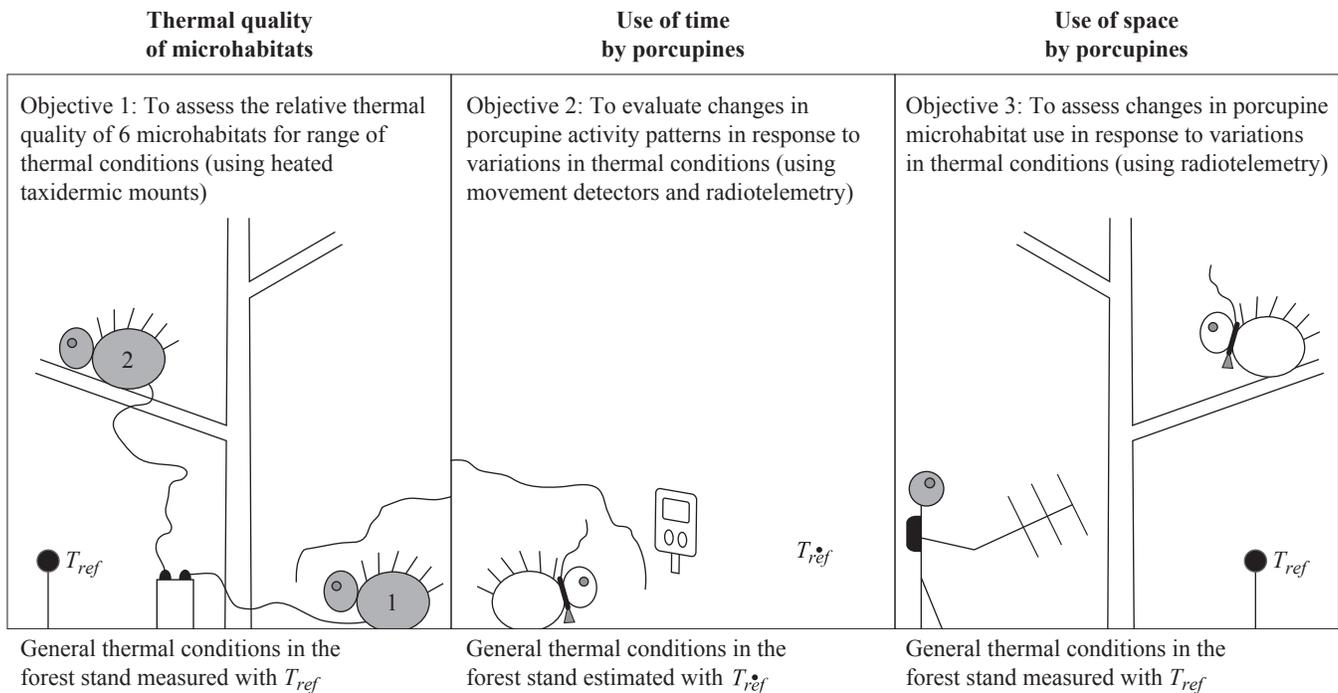


FIGURE 1. Study design evaluating the effects of thermal conditions on activity patterns and microhabitat use of North American porcupines, parc national du Bic, Quebec, 2004–2005. Objective 1: We used 2 heated taxidermic porcupine mounts to assess the relative thermal quality of 6 microhabitats: “den” (mount 1), “ground open”, “ground covered”, “conifer open”, “conifer covered”, and “deciduous” (mount 2), for a range of thermal conditions. Objective 2: We used movement detectors placed at the entrance of dens, radiotracking, and temperature recorders attached to porcupine radiocollars to evaluate changes in porcupine activity patterns in response to variations in thermal conditions. Objective 3: We used radiotracking to evaluate porcupine microhabitat use in relation to thermal conditions. Thermal conditions measured with T_{ref} (objectives 1 and 3) or estimated with T_{ref} (objective 2) (see Methods for details).

fragmented by abandoned and cultivated fields and characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest. The study population has been monitored each summer since 2000 and sometimes reached a high density (Mabille, Descamps & Berteaux, 2010). The population was at medium density and comprised about 40 individually marked porcupines in winter 2004 (see Berteaux, Klvana & Trudeau, 2005 for details on individual monitoring).

CHARACTERIZING THE THERMAL ENVIRONMENT IN THE STAND

We used a copper-constantan thermocouple placed inside a 4-cm-diameter, anodized aluminium black sphere to characterize the thermal environment (T_{ref}) in the forest stand where we assessed microhabitat thermal quality or made direct observations of porcupine behaviour (Figure 1, objectives 1 and 3). We positioned the thermocouple approximately 0.3 m above ground in a location randomly chosen in the stand where the mounts were placed or the radiocollared porcupines were observed. T_{ref} incorporates the effects of ambient temperature (T_a), convection, and radiation into a single variable and is roughly equivalent to the operative temperature (T_e , Winslow, Herrington & Gagge, 1937) that an animal would experience at this location. Because we could not measure T_{ref} continuously, T_{ref} was not available when evaluating how porcupines changed their activity patterns with variations in thermal conditions (Figure 1, objective 2). In this case, we used T_{ref}^* (an estimate of T_{ref}), calculated from continuous measurements of T_a and net radiation made at an automated weather station placed within the study site (Appendix I). T_a and net radiation explained 91% of the variance in T_{ref} (Appendix I), so we believe T_{ref}^* was a close estimate of T_{ref} and could be reliably used to characterize the thermal conditions in the stand.

RELATIVE THERMAL QUALITY OF THE MICROHABITATS (OBJECTIVE 1)

We used 2 heated taxidermic mounts to assess the relative thermal quality of 6 microhabitats (“den”, “ground open”, “ground covered”, “conifer open”, “conifer covered”, and “deciduous”) across the range of T_{ref} encountered through winter (see Appendix II for details on the fabrication and operation of the mounts and for a description of the 6 microhabitats). Use of heated mounts to quantify the metabolic heat production of free-living animals is debated (e.g., Walsberg & Wolf, 1996; Larochelle, 1998), so we did not use mounts for that purpose. We only used them to compare power consumption between microhabitats.

We placed each of the 2 mounts for about 24 h in a geographical site corresponding to 1 of the 6 microhabitats and then moved it to a new site. We always measured T_{ref} in the stand where the mounts were placed, so we could compare power consumption across microhabitats for similar T_{ref} conditions. A microhabitat was of better relative thermal quality than another when, for a given T_{ref} , a mount placed in that microhabitat consumed less power.

USE OF TIME AND SPACE BY PORCUPINES (OBJECTIVES 2 AND 3)

We fitted 26 adult porcupines (10 males, 16 females) with radio transmitters (Morin, Berteaux & Klvana, 2005) to measure porcupine use of time and space.

ACTIVITY PATTERNS (OBJECTIVE 2)

We attached temperature loggers (SmartButton Temperature Loggers, ACR Systems Inc., Surrey, British Columbia, Canada) to radio collars (total mass of collar with temperature loggers = 74 g) and fitted collars to porcupines while they were chemically immobilized (Morin & Berteaux, 2003). We tracked 14 porcupines carrying temperature loggers in 2004 and 6 in 2005. 3 individuals were tracked in both years. We used abrupt changes in temperature readings to estimate the timing of movements in and out of the dens. To complement data from temperature loggers, we placed movement detectors (Vigil 650X, Circuitronique Estrie Inc., Sherbrooke, Québec, Canada) at the entrances of used dens. Combining information from temperature loggers and movement detectors allowed us to determine when animals were inside or outside of a den (Appendix III). We validated our methodology by verifying the positions of porcupines once a day using telemetry.

We calculated time spent outside of the den, number and duration of activity bouts, and a nocturnality index representing the proportion of activity performed at night during a 24-h cycle. Time spent outside of the den corresponds to number of activity bouts \times duration of activity bouts. The nocturnality index varies from 0 (fully diurnal) to 1 (fully nocturnal). We did not consider variations in day length across winter (Zalewski, 2000) as this did not affect our results. Night started 30 min after sunset and ended 30 min before sunrise.

MICROHABITAT USE (OBJECTIVE 3)

We located 26 radiocollared porcupines twice a week by following the telemetry signal to the animal (homing). Porcupines are slow-moving animals that can be directly located by telemetry, thus allowing recording of the microhabitat use (Comtois & Berteaux, 2005; Morin, Berteaux & Klvana, 2005). Approach of the observer sometimes can disturb porcupine behaviour (Morin, Berteaux & Klvana, 2005), but experience allowed us to determine (from changes in the telemetry signal) if the animal was moving when approached ($n = 11$ occasions). We excluded those observations from analyses. We distributed our sampling scheme equally around the circadian cycle for each individual. Every time we located an individual, we measured T_{ref} in the stand where the porcupine was found and assigned the porcupine position to 1 of the 6 microhabitats. If the animal was in a tree, we also recorded its height (lower two-thirds *versus* higher third of tree) and position relative to the tree trunk (close to the trunk *versus* at the tip of a branch). We also noted whether the porcupine was feeding or resting.

DATA ANALYSES

RELATIVE THERMAL QUALITY OF THE MICROHABITATS (OBJECTIVE 1)

The 2 taxidermic mounts showed similar power consumption when exposed to similar thermal environments (results not shown). We thus pooled data from both mounts. We measured power consumption of mounts in 38 sites on 70 occasions (5 occasions in “den”, 14 in “ground open”, 13 in “ground covered”, 6 in “deciduous”, 12 in “conifer open”, and 20 in “conifer covered”). We averaged power consumed by the mounts and T_{ref} measurements over

1-h periods, excluding from analyses 1-h periods during which T_{ref} variation was > 3 °C. This ensured that meteorological conditions were rather uniform during measurements. We obtained 883 one-hour periods with both power consumption and T_{ref} measurements.

We fitted T_{ref} and microhabitat as covariates to test whether the power consumed by mounts (dependent variable) differed between microhabitats when accounting for T_{ref} . We also fitted $T_{ref} \times$ microhabitat as a covariate to test whether the effect of microhabitat on power consumed differed according to T_{ref} (e.g., to test whether the microhabitat offering the best thermal environment was the same at cold and warm T_{ref}). We first compared power consumption across all microhabitats sampled (Table I, model 1) and then compared groups of microhabitats that we expected to offer similar thermal conditions (Table I, models 2 to 4). We repeated measurements of power consumption on the same site on different occasions and, for a given site and occasion, at different hours, so we used linear mixed-effects models for analyses (proc MIXED, SAS software version 9.1, SAS, 2004). Mixed-effects models contain both fixed and random effects and use random effects to accommodate repeated measurements (Littell *et al.*, 1996).

USE OF TIME AND SPACE BY PORCUPINES (OBJECTIVES 2 AND 3)

Males are 20% heavier than females (D. Berteaux, unpubl. data), and sampling periods differed in 2004 and 2005, so we tested the effect of sex and year in all models before fitting other variables. We used mixed-effects models because data included repeated measurements on the same individuals (see Appendix IV for the structure of the models). Units for the effect sizes obtained from activity patterns and microhabitat use models can be complex (e.g., proportion of nocturnal activity per calendar day or activity bouts per °C). To facilitate reading, we thus did not indicate them. However, these units can be derived from the structure of models presented in Appendix IV.

Activity patterns (objective 2)

We examined how time spent outside of the den, number and duration of activity bouts, and the nocturnality index (dependent variables) varied with T_{ref} . Calendar date can influence activity (Vispo & Bakken, 1993) and was not independent from T_{ref} (Pearson correlation: $r = 0.65$, $P < 0.001$), whereas snow penetrability affects predation rates on herbivores in the boreal forest (Stenseth *et al.*, 2004), thus potentially influencing their activity patterns. To remove the effects of these potentially confounding variables, we included them as covariates in our models, together with their first-order interactions with sex. We measured snow penetrability daily (cm) in the study area using a Verme sinking-depth gauge calibrated at the start of the study using fresh porcupine tracks. Finally, we included in our model T_{ref} , T_{ref}^2 , and their first-order interaction with sex to test for thermal effects on activity and for possible differences between sexes in the response to T_{ref} (Appendix IV).

Microhabitat use (objective 3)

Although our aim was to examine how porcupines changed their use of 5 outside microhabitats with variations in thermal conditions, porcupines were found mostly in coniferous trees ($n = 257$ observations) when out of their den ($n = 268$ observations). This was consistent with observations of porcupine tracks found in the snow, which showed that porcupines in our study area did not feed on ground vegetation during winter (most of the vegetation was under the snow). Rather, porcupines restricted time spent on the ground and movements outside of their den, and snow tracks were generally very short (< 20 m) and led from the den to a nearby coniferous tree. We thus restricted our analyses of microhabitat use to the comparison of only 2 microhabitats: the “conifer open” ($< 25\%$ of vegetative cover around the animal) and “conifer covered” ($\geq 25\%$ of vegetative cover around the animal, see Appendix II) microhabitats. We tested whether use of tree cover (open *versus* covered microhabitat), height in tree, distance to trunk, and feeding behaviour were influenced by T_{ref} , T_{ref}^2 , and their first-order interaction with sex. T_{ref} only had an effect on feeding behaviour (see Results), so we further investigated the factors explaining the occurrence of feeding. To do so, we tested if the occurrence of feeding (0: no feeding, 1: feeding) was influenced by T_{ref} , T_{ref}^2 , tree cover around the porcupine, height in tree, distance to trunk, and their first-order interaction with sex (Appendix IV).

Results

RELATIVE THERMAL QUALITY OF THE MICROHABITATS (OBJECTIVE 1)

T_{ref} had a general negative effect on the power consumed by mounts (mean effect sizes \pm SE: -0.28 ± 0.02 , -0.28 ± 0.03 , -0.56 ± 0.08 , and -0.25 ± 0.04 $W \cdot ^\circ C^{-1}$ for models 1, 2, 3, and 4, respectively; see Table I for F and P -values). The relative thermal quality of microhabitats depended on T_{ref} as shown by the significant interaction between T_{ref} and microhabitat in model 1 (Table I).

Power consumption was generally lower inside than outside dens (-5.4 ± 2.7 W, $P = 0.049$, Table I, model 2). Dens thus offered the best microclimate for the range of T_{ref} considered (Figure 2). However, no mount happened to be in a den during the rare events when T_{ref} was > 0 °C (Figure 2). Power consumed by mounts was generally similar in terrestrial and in arboreal microhabitats (-0.6 ± 1.8 W, $P = 0.7$, Table I, model 3). However, power consumption increased more slowly in terrestrial than in arboreal microhabitats when T_{ref} decreased (0.33 ± 0.09 $W \cdot ^\circ C^{-1}$, $P < 0.001$, Table I, model 3). Finally, when comparing open and covered microhabitats, power consumed by mounts was generally lower in covered than in open microhabitats (-5.8 ± 2.0 W, $P = 0.004$, Table I, model 4). However, power consumption increased more rapidly in covered than in open microhabitats when T_{ref} decreased (-0.4 ± 0.1 $W \cdot ^\circ C^{-1}$, $P = 0.001$, Table I, model 4). At cold temperatures ($T_{ref} < -19.9$ °C), power consumed by mounts in arboreal or open microhabitats was about 25% higher than the power consumed inside dens (Figure 2).

ACTIVITY PATTERNS (OBJECTIVE 2)

TIME SPENT OUTSIDE OF THE DEN

Mean time spent outside of the den was 6.7 ± 0.5 h (range of individual means: 3.3 to 10.2 h, $n = 14$ individuals and 690 observations). The final model explaining time spent outside included a quadratic effect of T_{ref} , effects of several non-thermal variables (year, sex, calendar date, and snow penetrability) and 2 first-order interactions with sex ($T_{ref} \times \text{sex}$ and snow penetrability \times sex). Time spent outside increased with T_{ref} (0.49 ± 0.06 , $F_{1,669} = 38.1$, $P < 0.001$), increased more with T_{ref} at higher T_{ref} (0.011 ± 0.003 , $F_{1,669} = 15.2$, $P < 0.001$), and increased more with T_{ref} for males than for females (0.24 ± 0.04 , $F_{1,669} = 33.2$, $P < 0.001$; Figure 3).

Males spent more time outside dens than did females (5.9 ± 1.5 , $F_{1,12} = 16.4$, $P = 0.002$; Figure 3). Time spent by porcupines outside dens increased with calendar date (0.037 ± 0.007 , $F_{1,669} = 24.9$, $P < 0.001$), but decreased when snow penetrability increased (*i.e.*, when snow became softer, -0.23 ± 0.04 , $F_{1,669} = 29.9$, $P < 0.001$). The interaction between snow penetrability and sex arose because females were less sensitive to changes in snow penetrability: an increase in snow penetrability had a more important negative effect on time spent outside by males than by females (-0.13 ± 0.05 , $F_{1,669} = 5.8$, $P = 0.017$).

NUMBER AND DURATION OF ACTIVITY BOUTS

Mean number of activity bouts in a day was 1.40 ± 0.07 (range of individual means: 1.07 to 1.91, $n = 14$ individuals and 679 observations), and the mean duration of activity bouts was 5.0 ± 0.4 h (range of individual means: 2.8 to 7.3 h, $n = 14$ individuals and 966 observations). Number of activity bouts increased when T_{ref} decreased (-0.06 ± 0.01 , $F_{1,664} = 21.5$, $P < 0.001$, Figure 4) but was not affected by other variables. The duration of activity bouts depended on year, sex, T_{ref} , T_{ref}^2 , $T_{ref} \times \text{sex}$, calendar date, and snow penetrability. Males had longer activity bouts than females (3.8 ± 1.1 , $F_{1,12} = 11.4$, $P = 0.006$, Figure 4). The duration of activity bouts increased with increasing T_{ref} (0.43 ± 0.06 , $F_{1,946} = 34.6$, $P < 0.001$), increased more with T_{ref} at higher T_{ref} (0.006 ± 0.003 , $F_{1,946} = 6.6$, $P = 0.010$), and increased more with T_{ref} for males than for females (0.20 ± 0.04 , $F_{1,946} = 23.2$, $P < 0.001$, Figure 4). Activity bouts also lengthened with calendar date (0.021 ± 0.008 , $F_{1,946} = 7.4$, $P = 0.007$), but shortened when snow penetrability increased (-0.12 ± 0.03 , $F_{1,946} = 13.6$, $P < 0.001$).

NOCTURNALITY

The mean index of nocturnality was 0.48 ± 0.07 (range of individual means: 0.07 to 0.97, $n = 14$ individuals and 676 observations). Forty-eight percent of porcupines' active

TABLE I. Linear mixed effects models testing the effects of thermal conditions and microhabitat on power consumed by porcupine mounts, parc national du Bic, Quebec, 2004–2005. We first considered all 6 microhabitats sampled (model 1) and then compared groups of similar microhabitats (models 2 to 4). Models 1 and 2 are based on 883 measures of power consumption, while models 3 and 4 exclude measures in dens and are thus based on 791 measures.

Model	Categories of microhabitat, (n)	T_{ref}	Microhabitat	$T_{ref} \times \text{microhabitat}$
1	All available categories (6)	$F_{1,808} = 48.8, P < 0.001$	$F_{5,808} = 1.8, P = 0.1$	$F_{5,808} = 4.3, P < 0.001$
2	Den versus others (2)	$F_{1,813} = 73.4, P < 0.001$	$F_{1,813} = 3.9, P = 0.049$	Not significant†
3	Arboreal versus terrestrial (2)	$F_{1,725} = 77.1, P < 0.001$	$F_{1,725} = 0.1, P = 0.7$	$F_{1,725} = 12.7, P < 0.001$
4	Open versus covered (2)	$F_{1,725} = 62.8, P < 0.001$	$F_{1,725} = 8.2, P = 0.004$	$F_{1,725} = 10.9, P = 0.001$

† The full model (including $T_{ref} \times \text{microhabitat}$) showed this interaction was not significant. Model 2 thus only includes main effects of T_{ref} and microhabitat.

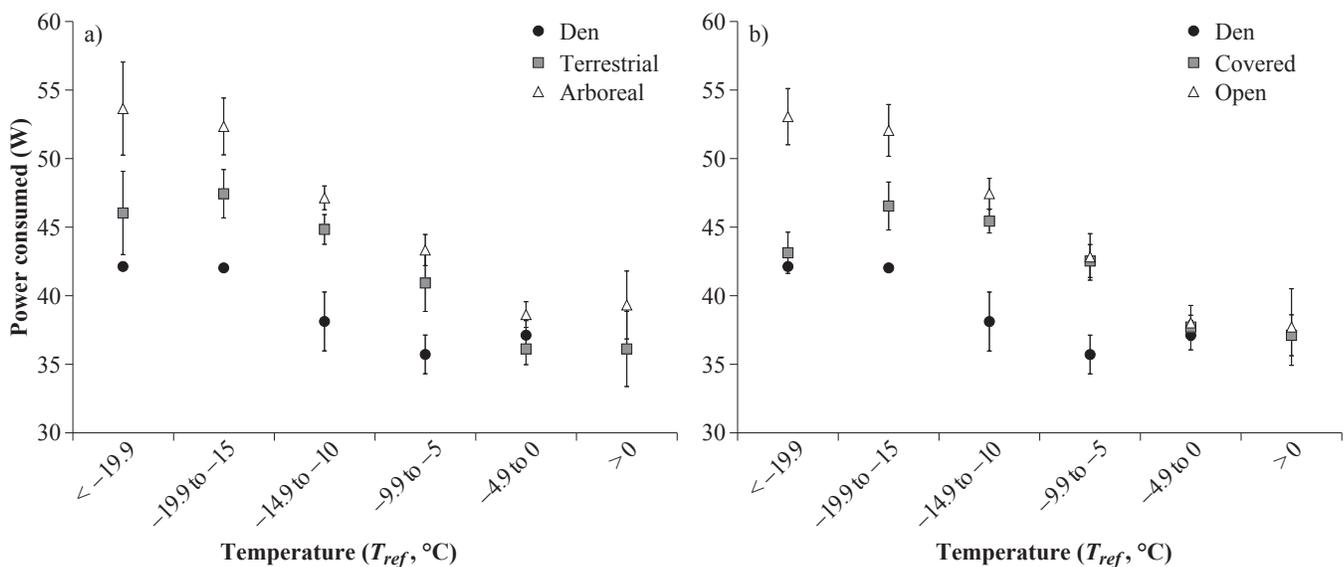


FIGURE 2. Power consumed (mean \pm SE) by porcupine mounts placed in different groups of microhabitats and exposed to variable thermal conditions, parc national du Bic, Quebec, 2004–2005. a) Dens, terrestrial, and arboreal microhabitats. b) Dens, covered, and open microhabitats. Porcupine mounts over-estimated the heat loss that real porcupines would encounter in similar thermal environments because mounts cannot use piloerection, vasoconstriction, or heat conserving postures. The reported powers thus cannot be used as rates of heat production for real porcupines.

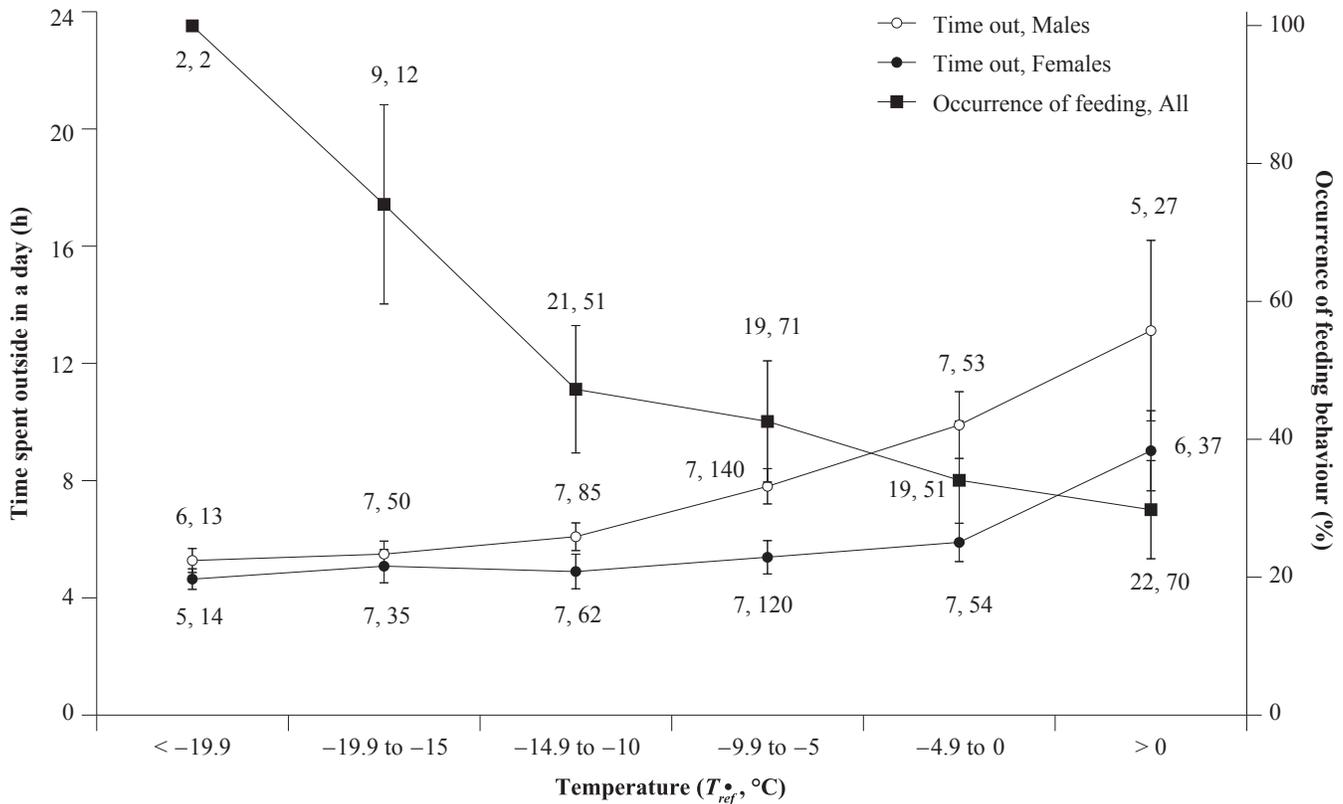


FIGURE 3. Time spent outside of a den in a day (mean \pm SE, left axis) and occurrence of feeding when in a conifer (mean \pm SE, right axis) as a function of thermal conditions (T_{ref}) for North American porcupines, parc national du Bic, Quebec, 2004–2005. Sample sizes (number of individuals, number of observations) are attached to each data point. We pooled data from males and females when there was no sex effect on the plotted variable.

time was thus during the night. The nocturnality index depended on calendar date, snow penetrability, and T_{ref} . Porcupines became less nocturnal when calendar date, and thus day length, increased (-0.007 ± 0.001 , $F_{1,659} = 101.3$, $P < 0.001$) and when snow penetrability increased (-0.009 ± 0.002 , $F_{1,659} = 13.8$, $P < 0.001$). Once those effects were taken into account, the nocturnality index still was influenced by T_{ref} , with porcupines being more nocturnal at higher T_{ref} (0.013 ± 0.002 , $F_{1,659} = 32.9$, $P < 0.001$).

MICROHABITATS USED OUTSIDE OF THE DEN (OBJECTIVE 3)

EFFECTS OF T_{REF}

Within conifers, T_{ref} had no significant effect on tree cover used by porcupines ($F_{1,230} = 0.05$, $P = 0.8$), on their height in trees ($F_{1,230} = 0.1$, $P = 0.7$), or on their distance to the trunk ($F_{1,230} = 2.9$, $P = 0.09$). However, occurrence of feeding increased when T_{ref} decreased (-0.07 ± 0.02 , $F_{1,230} = 10.7$, $P = 0.001$, Figure 3).

FACTORS EXPLAINING FEEDING BEHAVIOUR

Porcupines were feeding in conifers in $39.3 \pm 5.0\%$ of the observations. Occurrence of feeding was best explained by a model including T_{ref} , tree cover around the porcupine, and height of the porcupine in the tree. In addition to the negative effect of T_{ref} on occurrence of feeding (see above), feeding increased when porcupines were in “conifer open” ($51.0 \pm 9.9\%$ of observations) compared to “conifer covered” ($37.0 \pm 4.7\%$ of observations) microhabitats

(0.8 ± 0.3 , $F_{1,13} = 5.1$, $P = 0.041$) and when they were in the upper ($48.1 \pm 5.9\%$ of observations) rather than in the lower ($34.6 \pm 6.3\%$ of observations) part of trees (0.6 ± 0.3 , $F_{1,21} = 4.6$, $P = 0.043$).

Discussion

Dens offered the best protection against cold temperatures, in line with prediction 1. Outside of the den, terrestrial and covered microhabitats generally offered better thermal conditions than arboreal and open microhabitats, but the relative thermal quality of these microhabitats varied with thermal conditions, and some of the measured differences were low. This is only partially consistent with prediction 1.

Porcupines altered their patterns of den use and foraging behaviour according to thermal conditions. When it was cold, they reduced time spent outside of the den, increased the number of activity bouts per day, reduced the duration of activity bouts, became more diurnal, and fed more often when outside the den. This is generally consistent with prediction 2.

Outside of the den and within coniferous trees, porcupines did not change their microhabitat use according to thermal conditions. Rather, porcupines used microhabitats according to their activities: they used open microhabitats and the tops of trees when feeding and covered microhabitats and the bottoms of trees when resting. This contradicts

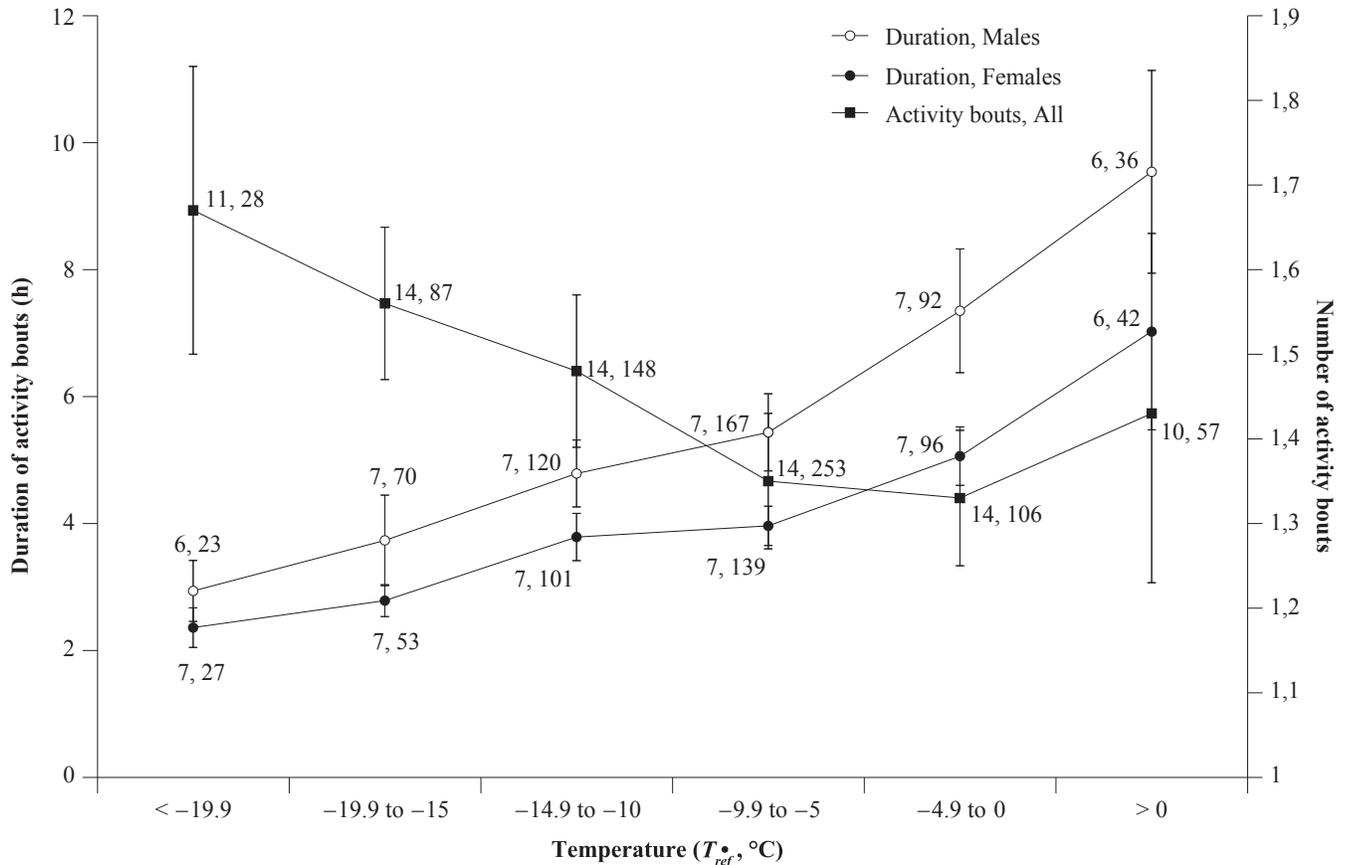


FIGURE 4. Duration of activity bouts (mean \pm SE, left axis) and number of activity bouts in a day (mean \pm SE, right axis) as a function of thermal conditions (T_{ref}) for North American porcupines, parc national du Bic, Quebec, 2004–2005. Sample sizes (number of individuals, number of observations) are attached to each data point. We pooled data from males and females when there was no sex effect on the plotted variable.

our prediction 3. We now discuss the physiological and ecological implications of these findings.

RELATIVE THERMAL QUALITY OF THE MICROHABITATS (OBJECTIVE 1)

The first step to study the physiological consequences of habitat selection is to characterize microclimates (Huey, 1991). The 25% difference in power consumption of mounts that we found when comparing microhabitats at low temperature should roughly correspond to the reduction of metabolic rate realized by porcupines when moving from a tree (or open microhabitat) to a den. Indeed, Fournier (1999) found a linear relationship between power consumption and the metabolic rate of porcupines kept below their lower critical temperature. They had calibrated porcupine mounts that had been built in the same way as ours. These results probably explain why den use seems so central to the behavioural thermoregulation strategy of porcupines.

We were surprised by the generally small differences in power consumption of mounts observed among microhabitats located outside of the den, especially between arboreal and terrestrial microhabitats (Figure 2). Others found relatively strong differences when comparing operative or standard operative temperatures in contrasted microhabitats (e.g., Melcher, Armitage & Porter, 1990). Wind speed and solar radiations were perhaps more homogeneous in

our winter forested landscape than anticipated. In addition, our measure of the thermal conditions in the stand was approximate because T_{ref} integrates the effects of wind only when solar radiation is present (see Appendix I). Similar T_{ref} measured either during the day or night could therefore correspond to different combinations of T_a , wind speed, and net radiation, and heated mounts may respond differently to those combinations. This may also partly explain why our study did not reveal clear differences in the power consumption of mounts in the outside microhabitats. Nonetheless, our results suggest that porcupines should experience a small decrease in thermoregulatory costs by feeding in favourable microhabitats. For example, feeding under cover during clear nights could limit exposure to an “intensely cold heat sink” (Clarke & Brander, 1973; Appendix V), that is the nocturnal winter sky, thereby saving energy by reducing heat loss.

ACTIVITY PATTERNS (OBJECTIVE 2)

Thermal constraints appeared to limit the time available to porcupines for aboveground activity, and porcupines compensated for this reduction in time spent outside by feeding increasingly often when T_{ref} decreased. Several species use plurimodal activity patterns and decreased activity time to avoid temperature extremes (e.g., Sharpe & Van Horne, 1999 on Piute

ground squirrels, *Spermophilus mollis*). However, predator avoidance may also lead animals to reduce their activities (Lima & Dill, 1990). Porcupines suffered high predation rates from fishers (*Martes pennanti*) during our study, and predation was linked to snow cover (Mabille, Descamps & Berteaux, 2010), probably because porcupines have short limbs and are thus vulnerable to predators when there is snow. In fact, porcupines spent less time outside of the den and had shorter activity bouts when snow penetrability was high, which may represent behavioural responses to increased predation risk.

North American porcupines and the related Hystricidae are essentially nocturnal (Roze, 1989; Roll, Dayan & Kronfeld-Schor, 2006). However, only 48% of the active time of porcupines was during the night, and porcupines were more diurnal at cold temperatures. Rodents living in cold environments are more likely to be diurnal, possibly because they exploit the warmer hours of the diel cycle (Roll, Dayan & Kronfeld-Schor, 2006). Porcupines also became more diurnal when snow penetrability increased. Given that fishers are primarily nocturnal and especially active at sunrise and sunset (Powell, 1993), a complementary hypothesis is that porcupines reduced the likelihood of encountering predators (Bakker *et al.*, 2005).

MICROHABITATS USED OUTSIDE OF THE DEN (OBJECTIVE 3)

When outside of dens, why did porcupines not modify their microhabitat use within coniferous trees according to thermal conditions? Part of the answer may lie in the relative thermal quality of outside microhabitats, which was less predictable than that of dens (see objective 1). In addition, because porcupines feed when outside of dens, choice of outside microhabitats may be driven by search for the most profitable food. For example, porcupines were hardly ever found in terrestrial microhabitats when outside of dens, and we believe this was primarily because food was essentially unavailable in those microhabitats. Within trees, leaf chemistry varies with exposure to solar radiation (Hirose, Werger & Van Rheeën, 1989), and open habitats and tree tops receive more light than other habitats. By feeding there, porcupines may access needles with higher nitrogen or energy content, and thus trade nutrition against thermoregulation (Torres-Contreras & Bozinovic, 1997). Alternatively (or in complement) porcupines may have been observed feeding more often when on top of trees because they were further from, and thus felt less disturbed by, the presence of the observer. However, we believe this hypothesis is unlikely to be correct because porcupines mostly seemed undisturbed by the observer's presence throughout our study. Instead, they may forage on tree tops because it lowers probability of detection by predators. These are testable hypotheses for future work.

SEX DIFFERENCES

Males increased their time spent outside faster than females when T_{ref}^* increased. Males are heavier than females and may thus be better protected against the cold (McNab, 1970). If being outside increased the probability of being detected by a predator (Lima & Dill, 1990; Blumstein, 1998), then males were more exposed to

predation than females. This may explain why an increase in snow penetrability had a more negative effect on the time spent outside by males than by females.

Our study measured how behaviour of a wild endotherm in winter may be driven by thermal conditions. It suggests, however, that behaviour is also influenced by constraints linked to food acquisition or predation risk. Even with sophisticated technology, disentangling the relative influences of these factors on the behaviour of wild animals remains challenging. Future progress will require rigorous testing through carefully planned experiments.

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Appendix I

Operation of the automated weather station used to continuously record weather conditions in parc national du Bic (Quebec, 2004–2005), and equation used to predict T_{ref} from weather measurements.

The automated weather station was located in an open field within our study site. It measured air temperature in the shade (T_a) using a temperature sensor (8-bit Temperature Smart Sensor, Hobo, Onset Computer Corp., Bourne, Massachusetts, USA) placed 1 m above ground, wind speed using a wind and direction sensor (Wind speed/Direction Smart Sensor, Hobo) placed 2 m above ground, and net radiation (0–100 μm) using a net radiometer sensor (model NR-Lite Net Radiometer, Kipp & Zonen, Delft, Netherlands) placed 1.5 m above ground. All sensors were connected to a datalogger (four-channel Micro-station, Hobo) that recorded information every minute. Some data on meteorological conditions measured during the study period are given in Appendix V. Because we recorded T_{ref} while operating heated mounts (objective 1), we could use synchronous measurements of T_{ref} , T_a , wind speed, and net radiation to establish an equation relating T_{ref} to the weather measurements made at the station. We only used daytime measurements to construct this equation because T_{ref} integrates the effects of wind only when solar radiation is present (Bakken & Gates, 1975). We tested whether T_a , the square root of wind speed (Kreith & Black, 1980), net radiation, and their first-order interactions influenced T_{ref} .

The best model explaining variations in T_{ref} includes effects of T_a ($F_{1, 86} = 268.6$, $P < 0.001$) and net radiation ($F_{1, 86} = 15.7$, $P < 0.001$) and is summarized as

$$T_{ref} = 0.004 + 0.906 \times T_a + 0.012 \times \text{net radiation} \quad [1]$$

with T_{ref} and T_a in $^{\circ}\text{C}$ and net radiation in $\text{W} \cdot \text{m}^{-2}$. We found no effect of wind speed on T_{ref} , possibly because wind speed at ground level in a forested stand was negligible. We calculated the percent of variance in T_{ref} explained (Pseudo R^2) as

$$\text{Pseudo}R^2 = 1 - \frac{\sum_i (y_i - \hat{y}_i)^2}{\sum_i (y_i - \bar{Y})^2} \quad [2]$$

with y_i being the actual value for observation i , \hat{y}_i being the predicted value for observation i , and \bar{Y} being the mean of all observed values. Equation 1 explained 91% of the variance in T_{ref} , and we used it to estimate T_{ref} from measurements of T_a and net radiation when measures of T_{ref} were not available (Figure 1, objective 2). Because we found no effect of wind speed on T_{ref} , we used equation [1] to estimate T_{ref} during both night and day.

Appendix II

Fabrication and operation of the heated taxidermic porcupine mounts used to assess the relative thermal quality of 6 microhabitats available to free-ranging North American porcupines in parc national du Bic, Quebec, 2004–2005.

Following Bakken, Erskine and Santee (1983) we built 2 heated taxidermic mounts in the form of North American porcupines. The size of the mounts was comparable to the size of southern Quebec porcupines, and we covered the copper core using pelts from animals that died naturally in our study area during winter 2003. We built the mounts in a standing posture with the head facing down. We lined the inside surface of the hollow copper mould with 24 gauge Teflon-coated iron wire that was connected to an external control circuit and to a Campbell CR-21X data logger (Campbell Scientific, Logan, Utah, USA). Electrical power was provided by four 6-V deep discharge batteries in series. Body temperature (T_b) of the mounts was regulated at 37.5 ± 0.3 $^{\circ}\text{C}$, which is the core body temperature of winter acclimatized free-ranging porcupines (D. W. Thomas, unpubl. data). We monitored temperature inside the copper mounts using a copper-constantan thermocouple placed in the centre of the mount. We wrote a program for the Campbell CR-21X to regulate T_b . Power was applied automatically as 24 V pulse to maintain body temperature. The datalogger measured voltage (V_m) every 5 s, calculated the power consumption (see below), and stored the mean power over 5-min intervals. We calculated the power drawn by each mount (P_m) from V_m and the resistance of the heater wire circuit (R) following equation [3]:

$$P_m = \frac{V_m^2}{R} \quad [3]$$

with P_m expressed in watts, V_m in volts and R in ohms. We measured T_{ref} continuously while operating the mounts by using a copper-constantan thermocouple placed inside an anodized aluminium black sphere and connected to the Campbell CR-21X data logger.

Our long-term study had established (D. Berteaux, unpubl. data) that porcupines wintering in our boreal forest environment could be found in 6 different microhabitats: “den”, “ground open”, “ground covered”, “conifer open”, “conifer covered”, and “deciduous”, detailed in the table below. We placed heated mounts horizontally in those microhabitats and compared power consumption between microhabitats for a range of T_{ref} in order to establish the relative thermal quality of those microhabitats. We visually estimated vegetative cover (percentage of the sky obscured by vegetation) within 1 m of the mount to classify microhabitats as open or covered.

APPENDIX II, TABLE I. Description of the 6 microhabitats available to North American porcupines in parc national du Bic, Quebec, 2004-2005. The 3 central columns of the table describe the categories we utilized to characterize microhabitat use by free-ranging animals and locations where we placed heated taxidermic porcupine mounts.

Microhabitat [†]	Den <i>versus</i> others [‡]	Arboreal <i>versus</i> terrestrial [‡]	Open <i>versus</i> covered [‡]	Description
Den	Den	NA	NA	Rock den regularly used by porcupines (mount placed 1 to 3 m from the entrance, depending on den structure)
Ground open	Others	Terrestrial	Open	On the ground, < 25% of vegetative cover
Ground covered	Others	Terrestrial	Covered	On the ground, ≥ 25% of vegetative cover
Conifer open	Others	Arboreal	Open	2 m above ground [§] in a coniferous tree, < 25% of vegetative cover
Conifer covered	Others	Arboreal	Covered	2 m above ground [§] in a coniferous tree, ≥ 25% of vegetative cover
Deciduous	Others	Arboreal	Open	2 m above ground [§] in a deciduous tree, vegetative cover always < 25% in winter

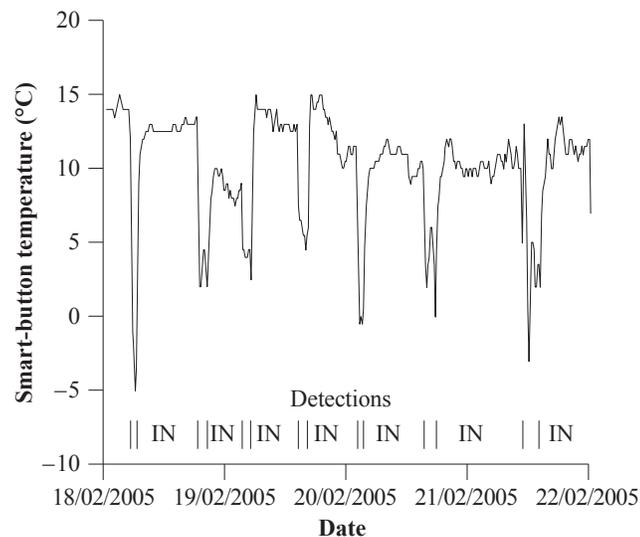
[†] Because we measured power consumption over extended periods of time, we could not determine whether the mounts were placed on the windward or leeward sides of a tree trunk, or in the sun or shade (these factors vary within a given day and were not taken into account).

[‡] We grouped microhabitats into categories for some analyses: den *versus* microhabitats other than dens, arboreal *vs* terrestrial microhabitats, open *versus* covered microhabitats.

[§] Real porcupines were generally higher in trees but we could not sample locations higher than 2 m because of technical difficulties.

Appendix III

Method used to determine movements of free-ranging North American porcupines in and out of dens in parc national du Bic, Quebec, 2004-2005. We combined information from temperature loggers and movement detectors to estimate the timing of movements in and out of the den as abrupt temperature changes concomitant with movement detections. We validated our methodology by verifying the positions of porcupines (*i.e.*, inside or outside the den) once a day using telemetry.



APPENDIX III, FIGURE 1. Example of temperature recordings made by Smart-button temperature loggers attached to North American porcupine radio collars in parc national du Bic, Quebec, 2004-2005. The figure also shows detections by movement detectors placed at the entrance of dens used by porcupines (bars at the bottom of the graph) and periods of time when we determined that the porcupine was inside its den ("IN").

Appendix IV

APPENDIX IV, TABLE I. Structure of the mixed-effects models testing the influence of T_{ref}^{\bullet} and T_{ref} on North American porcupine activity patterns (objective 2) and microhabitat use (objective 3), respectively. Calendar date was expressed in days, snow penetrability in cm, and T_{ref} in °C.

Dependent variable (unit) [†]	Variable type	SAS procedure	Independent variables	
			Fixed	Random
Activity patterns				
Time spent outside of den (h)	Continuous	MIXED	Year, Sex, Calendar date,	Porcupine identity
Number of activity bouts (1 / \geq 2 bouts)	Binomial	GLIMMIX	Snow penetrability, T_{ref}^{\bullet} , $T_{ref}^{\bullet 2}$,	
Duration of activity bouts (h)	Continuous	MIXED	Date \times Sex, Snow penetrability \times Sex,	
Nocturnality index	Continuous	MIXED	$T_{ref}^{\bullet} \times$ Sex, $T_{ref}^{\bullet 2} \times$ Sex	
Microhabitat use				
Tree cover around porcupine (“conifer open” / “covered”)	Binomial	GLIMMIX	Year, T_{ref}^{\bullet} , $T_{ref}^{\bullet 2}$, Sex, $T_{ref} \times$ Sex,	Porcupine identity
Height in tree (lower / upper canopy)	Binomial	GLIMMIX	$T_{ref}^{\bullet 2} \times$ Sex	
Distance to trunk (close / far from trunk)	Binomial	GLIMMIX		
Feeding behaviour [‡] (no feeding / feeding)	Binomial	GLIMMIX		

[†] When the dependent variable was binomial, we specified the 2 levels (between parenthesis) considered in analysis.

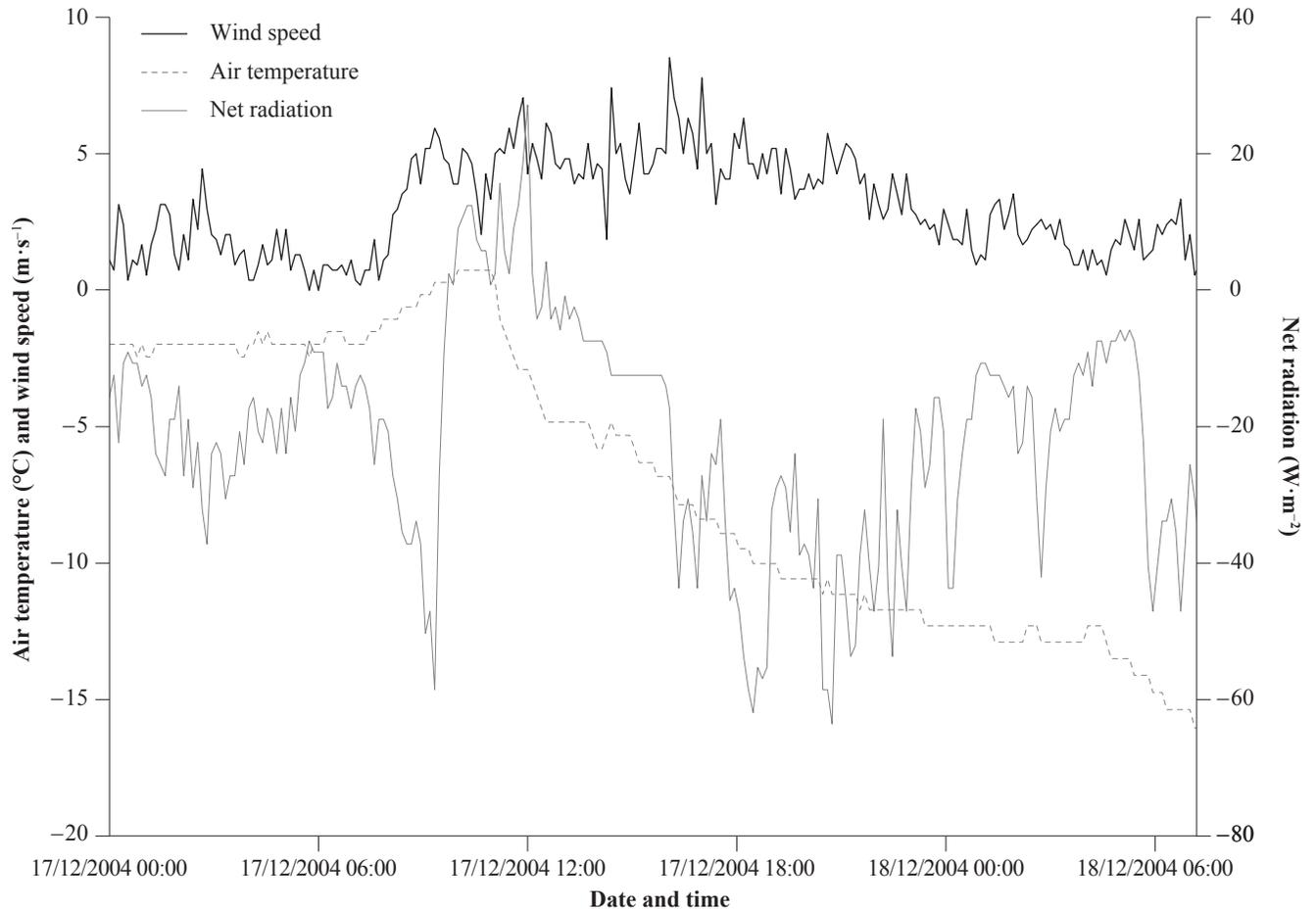
[‡] Because T_{ref}^{\bullet} had a significant effect on feeding behaviour (see Results), we further investigated factors explaining the occurrence of feeding by testing whether Tree cover around the porcupine, Height in tree, Distance to trunk, Sex, Tree cover \times Sex, Height in tree \times Sex, and Distance to trunk \times Sex also had an effect on feeding behaviour.

Appendix V

APPENDIX V, TABLE I. Meteorological conditions recorded by the automated weather station located in parc national du Bic, Quebec, in 2004 (12 January to 16 April) and 2005 (13 December 2004 to 19 March 2005). Monthly means are given with minimum and maximum monthly values in parentheses.

	Air temperature (°C)		Wind speed (m·s ⁻¹)		Net radiation (W·m ⁻²)	
	2004	2005	2004	2005	2004	2005
December		-9.4 (-19.5 to +11.0)		2.6 (0 to 11.5)		-18.6 (-593.0 to +274.6)
January	-16.6 (-27.1 to -7.9)	-12.8 (-27.1 to +10.2)	3.1 (0 to 8.2)	2.5 (0 to 8.9)	-15.7 (-71.8 to +119.6)	-22.7 (-106.4 to +154.2)
February	-9.0 (-27.1 to +1.6)	-9.7 (-26.1 to +4.2)	2.3 (0 to 10.4)	NA [†]	-16.0 (-118.0 to +188.9)	-17.1 (-287.8 to +159.2)
March	-3.6 (-21.0 to +11.8)	-6.6 (-17.4 to +5.0)	2.2 (0 to 9.3)	NA [†]	+8.7 (-263.1 to +543.5)	-8.9 (-497.3 to +264.7)
April	+0.6 (-3.9 to 6.6)		2.1 (0 to 8.7)		+27.9 (-550.1 to +612.8)	

[†] NA: Not Available, wind speed sensor was out of order during that period.



APPENDIX V, FIGURE 1. Examples of air temperature, wind speed, and net radiation recordings made at the automated weather station installed within our study site in parc national du Bic, Quebec, 2004-2005. Data on air temperature and net radiation were used to estimate T_{ref}^* , when measurements of T_{ref} were not available. The figure shows how meteorological conditions could vary within a relatively short time period. In particular, it shows how net radiation varies from negative values at night (when sky constitutes a heat sink) to positive values during the daytime.