

Hierarchical habitat selection by North American porcupines in southern boreal forest

Patrick Morin, Dominique Berteaux, and Ilya Klvana

Abstract: In habitat-selection studies, a multi-scale approach is considered necessary to ensure that all elements of selection are depicted and that management decisions accurately reflect the needs of the species under study. We examined hierarchy in summer habitat selection in North American porcupines (*Erethizon dorsatum* (L., 1758)) in Eastern Canada at the scales of landscape, home range, and single tree. We used radiotelemetry to locate and observe animals visually to record their behaviour and exact location in the habitat. Den use in summer was unexpectedly high for some of our animals, which forced us to use a restricted number of locations per individual for comparison among scales. Although porcupines are generalists at the landscape level, selection patterns appear at the home-range and tree levels. Human-used land and conifer forests were least selected features of home ranges, while deciduous forests dominated by trembling aspen (*Populus tremuloides* Michx.) and mixed forests were most selected. At the tree scale, trembling aspen was found to be selected over other deciduous trees. However, fruit-producing trees were even more selected. This study shows the importance of a multi-scale approach that includes fine-scale selection.

Résumé : Dans les études de sélection de l'habitat, une approche multi-échelles est nécessaire afin de s'assurer que tous les éléments de sélection sont décrits et que la gestion reflète précisément les besoins de l'espèce étudiée. Nous avons examiné la hiérarchie dans la sélection de l'habitat estival chez le porc-épic d'Amérique (*Erethizon dorsatum* (L., 1758)) dans l'Est du Canada aux échelles du paysage, du domaine vital et de l'arbre. La radio-téléométrie a servi à localiser et observer les animaux visuellement de façon à noter leur comportement et leur position exacte dans l'habitat. L'utilisation estivale des tanières était exceptionnellement élevée chez certains animaux, ce qui a entraîné l'utilisation d'un nombre restreint de localisations par individu pour comparer les échelles de sélection. Quoique les porcs-épics soient généralistes au niveau du paysage, des patrons de sélection apparaissent aux niveaux du domaine vital et de l'arbre. Les milieux anthropiques et les forêts conifériennes étaient les éléments des domaines vitaux les moins prisés, alors que les forêts feuillues dominées par le peuplier faux-tremble et les forêts mixtes étaient préférées. À l'échelle de l'arbre, le peuplier faux-tremble (*Populus tremuloides* Michx.) était préféré aux autres feuillus, à l'exception des arbres fruitiers qui l'étaient davantage. Cette étude démontre l'importance d'une approche multi-échelles qui inclut la sélection à l'échelle fine.

Introduction

Issues of scale and spatial hierarchy have become a primary focus in ecological research (Wiens 1989), and have been increasingly considered in habitat-selection studies (Johnson 1980; Schaefer and Messier 1995; Rettie and Messier 2000; Rolstad et al. 2000; Chamberlain et al. 2002). Habitat selection, defined as the use of a habitat component disproportionately to its availability, was conveniently ordered through spatial scales by Johnson (1980). First-order selection is the selection of the distribution range of a species. Second-order selection is the process through which an individual selects its home range within the landscape.

Third-order selection relates to the selection of the habitat components (e.g., forest stands) within the home range. Finally, fourth-order selection is the selection of an item (e.g., a food item) or microhabitat among available ones within the habitat component selected at the third order (Johnson 1980). These orders are hierarchical because what is available at each order depends on the use at the order below.

Habitat selection is not necessarily congruent across scales (McLoughlin et al. 2002; 2004). In other words, patterns observed at one scale are not necessarily good predictors of patterns obtained at other scales. For example, a species feeding preferentially on a given plant might not select, at a higher spatial scale, the habitats where this plant is the most abundant. This can occur if the best feeding habitats do not satisfy other needs such as shelter. Conflicting demands may thus lead to selection criteria that vary across scales (Fortin et al. 2003). To date, examples of congruence of habitat selection across spatial scales have been shown in some study systems (e.g., Ward and Saltz 1994; Schaefer and Messier 1995; Mysterud et al. 1999) and not in others (e.g., McLoughlin et al. 2002; Boyce et al. 2003; Fortin et al. 2003; McLoughlin et al. 2004). It is not yet clear how the

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presence or absence of congruence can be predicted. Understanding which factors organize the hierarchy of selection across scales is clearly a critical step in habitat-selection research and has important practical implications for habitat management. Rettie and McLoughlin (1999) proposed that decisions at coarser scales should reveal environmental factors that are most important to fitness than decisions at finer scales. More specifically, Senft et al. (1987) suggested that the relative importance of plant–herbivore interactions may decline at larger spatial scales, as abiotic factors increase in importance.

We studied the congruence of habitat selection across spatial scales using the North American porcupine (*Erethizon dorsatum* (L., 1758)) as a study model. Porcupines are convenient models for such studies because they are relatively slow-moving animals, and thus can be precisely localized using radiotelemetry on foot. In addition, porcupines are mostly arboricolous–folivorous in the summer time, therefore food items (e.g., tree leaves) chosen by individuals can easily be identified. This allowed us to study with a single technique (i.e., classical radiotelemetry) all the orders of selection defined by Johnson (1980).

Habitat use by porcupines has been studied throughout North America (e.g., Marshall et al. 1962; Gill and Cordes 1972; Harder 1980; Roze 1987; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001). Previous studies have often focused on tree selection, especially during winter. The porcupine is described as a generalist herbivore at the species level, exhibiting selective herbivory at the individual level (Snyder and Linhart 1997). Habitat selection by the porcupine at the landscape, home-range, or stand level has rarely been examined (but see Harder 1980; Griesemer et al. 1998). The link between habitat selection at various levels therefore remains to be understood for this species. Porcupines use existing cavities (e.g., rock cavities, tree stumps, hollow trees, culverts, underneath buildings) as dens in winter (Marshall et al. 1962; Roze 1984; 1987; Griesemer et al. 1996; 1998) and sometimes in summer (Roze 1989). Dens allow predator and biting insect avoidance, social interactions, and have a thermal function (Griesemer et al. 1996).

In this paper our main objective is to test whether porcupines exhibit different patterns of habitat selection at three spatial scales during summer. We therefore assessed habitat selection at the second, third, and fourth orders of selection simultaneously.

Materials and methods

Study area

We worked in Parc National du Bic (68°46'W, 48°21'N), on the south shore of the St. Lawrence River estuary, Quebec, Canada (Fig. 1). The study area is characterized by its rugged topography. Its porcupine population is known to sometimes reach a high density (ca. 40 individuals/km² when the study was performed; D. Berteaux, unpublished data), with marked and regular fluctuations of abundance (Klvana et al. 2004).

Habitat was fragmented by agriculture and logging into small patches ranging from cultivated fields to deciduous,

mixed, and coniferous forests. Present human activities (tourism) are concentrated along roads, bike trails, and the park administration buildings, which together represent 2.0% of our study area. Trembling aspen (*Populus tremuloides* Michx.; hereinafter called aspen), eastern white cedar (*Thuja occidentalis* L.; hereinafter called cedar), white spruce (*Picea glauca* (Moench) Voss), and balsam fir (*Abies balsamea* (L.) P. Mill.) are the dominant tree species that respectively represent 28%, 16%, 16%, and 15% of the total basal area. The presence of serviceberry (species of the genus *Amelanchier* Medik.) and American mountain ash (*Sorbus americana* Marsh.) along forest edges is noteworthy, as porcupines in our study site are fond of their fruits. Our study area belongs to the eastern balsam fir – yellow birch (*Betula alleghaniensis* Britt.) ecological domain of the mid-Appalachian hills ecological region (Grondin et al. 1999).

Study design

Animal needs vary in time and habitat selection is season-dependent. We worked during the summer season and defined summer biologically according to the porcupine's life history in our region. Preliminary observations in 2000 showed that porcupines fed predominantly on aspen leaves in summer. Aspen leaves open in late May (Berteaux et al. 2005), which defined the start of summer for this study. In late August, porcupines shifted a portion of their diet to the fruits of mountain ash, so we defined the end of the summer period as the 3rd week of August, just before fruits became available.

To ensure the spatial accuracy of our data, we used direct observations of radio-tagged individuals instead of triangulation (Garshelis 2000). This approach also allowed us to record the behaviour of animals at each location and to assess their use of the microhabitat.

Capture and marking

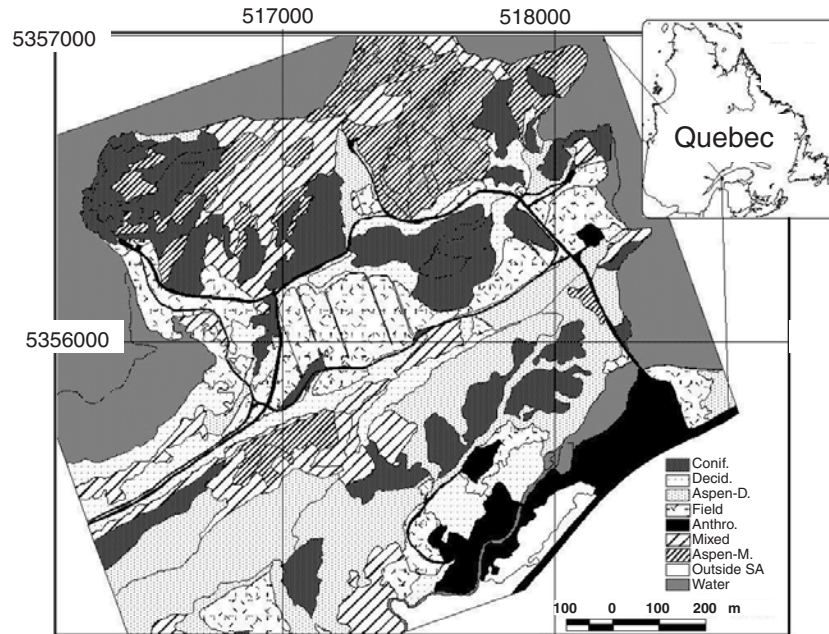
We captured porcupines from 19 January to 21 May 2001 throughout our study area and immobilized individuals by intramuscular injection in the tail of a mixture of 5 mg/kg of ketamine hydrochloride and 2 mg/kg of xylazine hydrochloride (Morin and Berteaux 2003). We ear-tagged all animals and equipped a sample of individuals with a Lotek SMRC-5RB VHF transmitter (Lotek Wireless Inc., Newmarket, Ontario) mounted on a leather collar. Capture techniques and immobilization procedures were approved by the McGill Animal Care Committee (Animal Use Protocol project No. 4213) and the Société de la Faune et des Parcs, Gouvernement du Québec (permit No. 20000417-001-01-S-P).

Telemetry

We acquired telemetry locations at regular intervals and a given individual was never located twice in a 24-h period. We performed telemetry day and night to distribute our sampling scheme equally around the circadian cycle for each individual.

Each time we located an animal using telemetry, we followed the signal to the individual and performed a visual observation of the porcupine. We obtained UTM coordinates from a hand-held global positioning system (GPS). If we

Fig. 1. Location of our study area in Parc National du Bic, Quebec, Canada (68°46'W, 48°21'N), and vegetation map created for our study of habitat selection in the North American porcupine (*Erethizon dorsatum*). Habitat types as described in Table 1 are as follows: Conif., conifer forest; Decid., deciduous forest; Aspen-D., trembling aspen dominated deciduous forest; Field, fields; Anthro., human-used land; Mixed, mixed forest; Aspen-M., trembling aspen dominated mixed forest. Outside SA and Water refer to terrestrial habitats located outside the study area and to water habitats unavailable to porcupines, respectively. The grid displays UTM coordinates (zone 19N).



could not see the animal because it was in a deep den or in a tree with dense foliage, we could still ascertain its geographic position within a 5–10 m radius with our telemetry equipment. This allowed us to record which microhabitat an animal was using (underground or in a tree), whether the animal could be seen or not. Each time we located a porcupine in a den, we assigned a unique number to the den. We recorded den type (rock crevice, tree stump, hollow tree, culvert, or building) and assigned to each den a subjective den-quality index (low quality: the porcupine could be reached by hand; medium quality: the porcupine could be seen but not reached by hand; best quality: the porcupine could not be seen). We assumed depth of dens to be an indicator of their quality because deeper dens offered better protection against predators, biting flies, and temperature extremes.

Habitat description

Porcupines are primarily tree-dwelling animals in summer, using trees almost exclusively when feeding or resting outside of their dens. They largely base their choice of food on tree species (Griesemer et al. 1998; Zimmerling and Croft 2001) and use ground vegetation only when they venture out of the forest to feed in adjacent fields. Therefore, an accurate knowledge of tree species dominance in each stand was necessary to describe available habitats. We created a forest map with a high cartographic resolution to represent the high forest heterogeneity, but we used a relatively simple classification of vegetation.

To create our map, we used a 1:3000-scale aerial photograph taken in 1993 (Photocartotheque Québécoise, Charles-

bourg, Quebec) scanned at high resolution. This image was imported into the Cartalinx software (Clark Labs 1999), where we outlined all the zones of different tree cover. For our 1.82-km² study area, we obtained 146 polygons (mean (\pm SE) area = 1.25 \pm 0.14 ha, range = 0.0057–1.43 ha), which suit the heterogeneity of the landscape closely.

To ground-proof this map and to determine the proportion of tree species for each polygon, we sampled 90 of the 112 forest polygons outlined in our study area. The remaining 22 forest polygons were assigned to a vegetation class based on the aerial photograph and our knowledge of the landscape. Species and basal area of trees with a diameter at breast height greater than 9 cm (Potvin et al. 1999) were measured using a factor-2 prism (Grosenbaugh 1952) at two stations 20 m apart for each sampling point. The 34 remaining polygons did not require sampling, as they were either fields, roads, trails, or buildings.

Because trembling aspen is by far a porcupine's preferred food source (Roze 1989, P. Morin and D. Berteaux, unpublished), we classified habitats according to the abundance of this species (Table 1).

Data analyses

We imported the vegetation polygons and the vegetation survey data into Idrisi32 GIS software (Clark Labs 2000) to create the vegetation map (Fig. 1). To calculate 100% minimum convex polygons (MCP) (Mohr 1947), we used the "Animal movements" extension version 2.04 (Hooge and Eichenlaub 1997) to ArcView[®] version 3.2a (Environmental Systems Research, Inc. 1998). We outlined our study area by

Table 1. Vegetation classification scheme used to create a habitat map for the second and third orders of selection of North American porcupines (*Erethizon dorsatum*) in Parc National du Bic, Quebec, Canada.

Criteria 1	Criteria 2	Vegetation type	Code	Number of polygons	Area (ha)	Percentage of area
Trembling aspen $\geq 50\%$ *	Conifers $< 20\%$	Deciduous forest (trembling aspen dominated)	Aspen-D.	14	29.9	15.3
	Conifers $> 20\%$	Mixed forest (trembling aspen dominated)	Aspen-M.	22	30.7	15.7
	Deciduous $< 20\%$	Conifer forest	Conif.	33	46.3	23.8
Trembling aspen $< 50\%$	Conifers $< 20\%$	Deciduous forest	Decid.	23	22.7	11.7
	Deciduous $> 20\%$	Mixed forest	Mixed	17	31.3	16
	Conifers $> 20\%$	Mixed forest	Mixed	28	30.2	15.5
No trees	Fields	Fields	Field	9	3.9	2
	Roads, trails, buildings	Human-used land	Anthro.			

Note: The number of polygons, total area (ha), and proportion (percentage) of the study area covered is given for each habitat type.

*Percentage of the total basal area of trembling aspen, *Populus tremuloides*, in each polygon.

taking the MCP of all locations. This method assumes that all animals have equal access to all these resources, which may not necessarily be the case (Garshelis 2000). Nevertheless, we chose the MCP because it is an objective method that is widely used in habitat-selection studies and thus facilitates comparison with other studies.

Individual home ranges were outlined using the MCP method. Girard et al. (2002) found that the MCP method consistently underestimated home ranges, as opposed to kernel and cluster estimators that tend to overestimate home ranges to varying degrees. As recommended by Stone et al. (1997), we used topographic home ranges, which were computed using the "Surface tools for points, lines and polygons" extension version 1.3 (Jenness 2001). The XTools extension version 6/1/2001 (DeLaune 2001) was used to extract information, such as vegetation data within home ranges, from the different maps.

At the study-area scale (second order), we compared the proportion of each habitat type within individual home ranges to the availability of these habitats within the entire study area. At the home-range scale (third order), we compared the proportion of locations in each habitat type for each porcupine to the relative availability of habitat types within its home range. At the fourth order of selection, we analyzed selection by comparing tree species used by porcupines with the average proportion of tree species in the vegetation polygons used by porcupines (availability). We had to redefine categories of available resources at this scale, because tree species rather than vegetation types were the unit of interest. We used our knowledge of porcupine natural history to define the following categories of available resources: aspen, cedar, conifer (all conifers species except cedar), fruit-bearing trees (serviceberry and American mountain ash), and deciduous trees (all deciduous species except aspen and fruit trees). Note that we lumped several tree species in the same category when we had no a priori indication that porcupines behaved differently according to these species. Cedars formed a category on their own, as they may be used as a refuge against biting insects (Marshall et al. 1962).

Statistical analyses

Individuals (not locations) were the sampling unit at all scales. We analyzed habitat selection at each scale using an adaptation of the Aebischer method (Aebischer et al. 1993), which is described in Crête et al. (2001). This method uses a MANOVA (i.e., Hotelling's test; SAS Institute Inc. 1991), but without the log-ratio transformation proposed by Aebischer et al. (1993). There is a controversy about the effectiveness of this ratio transformation within the statistical community (Crête et al. 2001). Distribution of residuals was multivariate normal (Mardia 1975).

We proceeded in three steps. In addition to testing for selection/avoidance of each habitat type, Hotelling's test simultaneously verifies over all habitat types for random habitat use (first step). The effect of sex was included in this analysis. When we detected a significant difference between use and availability (i.e., percent use – percent availability calculated for each animal), we used one sample *t* tests (second order) or paired one sample *t* tests (third and fourth orders) to determine which habitats were selected or avoided (second step). The results obtained show selection (use supe-

Table 2. Distribution of observations made with respect to the location of the porcupine in the habitat (ground or <1 m from the ground, tree, den, or unknown) and its behaviour (feeding, resting, travelling, disturbed, or unknown).

	Feeding	Resting	Travelling	Disturbed	Unknown
Ground	4	3	6	32	3
Tree	33	140	7	51	14
Den	0	135	0	0	0
Unknown	0	0	0	0	5

Note: “Disturbed” indicates that the behaviour of the porcupine had probably been affected by the observer’s presence, and thus could not be recorded without bias. Porcupines localized in dens were assumed to be resting.

rior to availability) or avoidance (use inferior to availability) of habitat types. When significantly nonrandom use was found, habitats were finally ranked with respect to each other (third step) as suggested by Johnson (1980) and Aebischer et al. (1993). In the rankings, “>” indicates selection of a resource over another, while “>>>” indicates a significant selection of a resource over another.

Since we analyzed habitat selection at the fourth order in terms of tree species or groups of trees species, data were missing at this spatial scale when we found porcupines in dens. This generated a problem when comparing selection across scales, because the data set used to analyze selection at the second and third orders of selection was different from the data set used at the fourth order. To circumvent this problem, we performed two habitat-selection analyses at the second and third orders: a first analysis using the complete data set and a second analysis using a restricted data set (hereinafter called no den data set) in which observations in dens were excluded. We compared results from the two analyses before analysing the hierarchy across the three scales of selection.

Differences between sexes in mean home-range size and proportion of observations in dens were tested with Mann–Whitney *U* tests because the normality assumption was always violated (Fowler et al. 1998). Throughout our analyses, we used a significance level of 0.05 to reject the null hypothesis. Results are expressed as means \pm SE.

Results

We followed 17 adult porcupines (9 females, 8 males) from 28 May 2001 to 21 August 2001 and obtained 22–31 locations per animal (25.5 ± 0.5 , $n = 433$). This is slightly above the minimum number recommended by Aebischer et al. (1993) for habitat-selection studies. We made visual contact with the focal individual 275 times, yet we could localize and sometimes determine the behaviour of a porcupine without seeing it. Porcupines could be localized in the habitat (ground, tree, or den) under most circumstances (Table 2). Their behaviour was recorded as feeding, resting, travelling, but sometimes their behaviour could not be determined (Table 2). Our results confirm that porcupines are mostly solitary in summer, as only 3.7% ($n = 433$) of our observations were made on individuals found to be within 5 m of another individual. Home ranges were highly variable in size. There was no significant difference in home-range size between males and females (males: 20.9 ± 5.8 ha, range

6.0–58.4 ha; females: 15.4 ± 5.6 ha, range 1.5–58.8 ha; Mann–Whitney *U* test, $U = 22.00$, $P = 0.178$).

Den use

We found porcupines in a den 135 times (31.2% of locations). Consequently, the no den data set includes 298 observations. The 17 porcupines used 87 different den sites, which were all rock caverns that are present in great numbers on mountain flanks of our study area. Porcupines used low-quality dens 3.8% of the time, medium-quality dens 6.9% of the time, and high-quality dens 88.5% of the time. Any given den was used at a relatively low frequency: 63.2% of dens were used 1 time, 25.3% were used 2 times, 4.6% were used 3 times, and only 4.5% were used ≥ 4 times ($n = 87$ dens). Porcupines changed dens very often: 51.2%, 38.8%, 7.0%, and 3.1% ($n = 131$) of observations corresponded to dens used 1 time, 2 times, 3 times, and 4 times by the same individual, respectively. There was a large variation in the extent to which individuals used dens. Some porcupines were found in a den 70% of the time, whereas others were never observed in dens (proportion of locations in dens = $31.9\% \pm 5.9\%$, range 0%–69.6%, $n = 17$). Females were found in dens twice as often as males, but the difference was not significant (females: $41.6\% \pm 7.3\%$, $n = 9$; males: $21.1\% \pm 8.9\%$, $n = 8$; Mann–Whitney *U* test, $U = 53.00$, $P = 0.1$).

Habitat selection

Second order of selection

Complete data set — Use of habitat types was not significantly different from random (Wilk’s $\lambda = 0.75$, $F_{[6,11]} = 0.60$, $P = 0.72$; Fig. 2a) and there was no effect of sex (Wilk’s $\lambda = 0.52$, $F_{[6,10]} = 1.53$, $P = 0.26$).

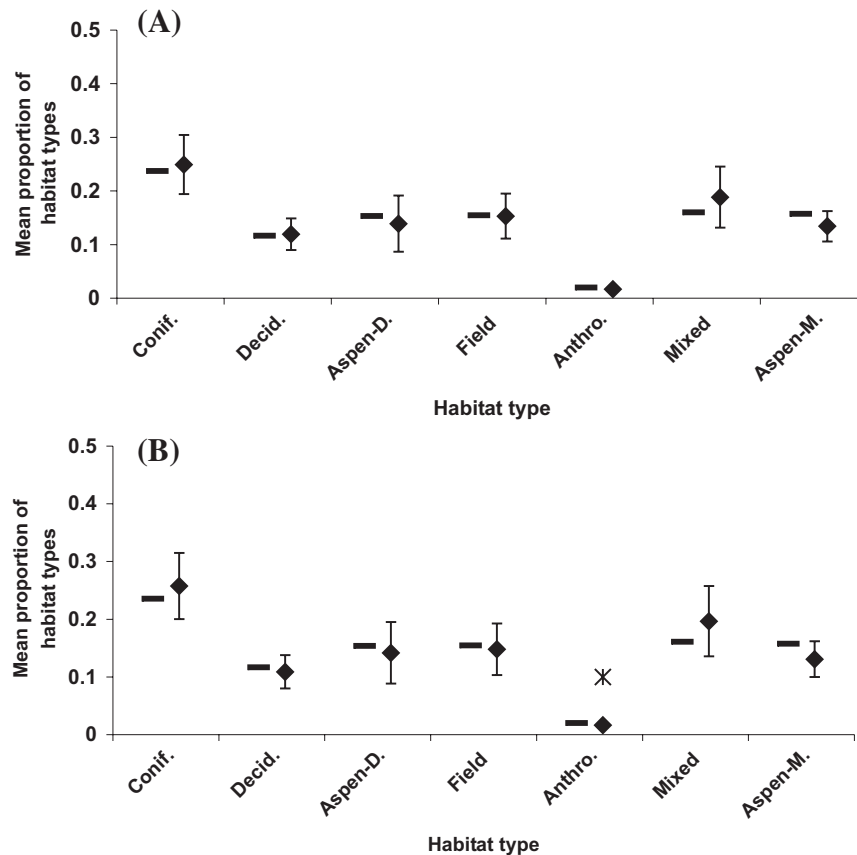
No den data set — Use of habitat types was not significantly different from random (Wilk’s $\lambda = 0.75$, $F_{[7,10]} = 0.46$, $P = 0.84$; Fig. 2b) and again there was no effect of sex (Wilk’s $\lambda = 0.51$, $F_{[7,9]} = 1.20$, $P = 0.39$).

Third order of selection

Results at the third order of selection differed from results at the second order of selection, as habitat use was not random and we detected significant selection or avoidance for several habitat types.

Complete data set — Use of habitat types was not random (Wilk’s $\lambda = 0.21$, $F_{[6,11]} = 7.05$, $P = 0.003$). There was no significant effect of sex on selection at this scale (Wilk’s $\lambda = 0.59$, $F_{[6,10]} = 1.16$, $P = 0.40$). Trembling aspen dominated deciduous forest ($t = 3.05$, $P = 0.0077$) and mixed forest ($t =$

Fig. 2. Mean proportion of habitat types (Conif., conifer forest; Decid., deciduous forest; Aspen-D., trembling aspen dominated deciduous forest; Field, fields; Anthro., human-used land; Mixed, mixed forest; Aspen-M., trembling aspen dominated mixed forest) in the study area (bars indicate habitat availability) against their proportion in porcupine home ranges (diamonds indicate habitat use) for the complete data set (A) and the no den data set (B). Standard errors are shown for habitat use. There are no standard errors for available habitat at this scale, as it is constant for all animals. An asterisk indicates statistically significant selection or avoidance ($P < 0.05$).



2.26, $P = 0.038$) were significantly selected, and conifer forest ($t = -3.11$, $P = 0.0067$), fields ($t = -3.96$, $P = 0.002$) and human-used land ($t = -4.67$, $P = 0.003$) were significantly avoided. Deciduous forest was not significantly selected ($t = 1.53$, $P = 0.15$) and aspen-dominated mixed forest was not significantly avoided ($t = -0.71$, $P = 0.49$) (Fig. 3a). Habitats were ranked as follows: Aspen-D. > Mixed >>> Decid. > Aspen-M. >>> Conif. > Field > Anthro. (codes are described in Table 1).

No den data set — Use of habitat types was not random (Wilk's $\lambda = 0.26$, $F_{[7,10]} = 4.02$, $P = 0.02$). There was no significant effect of sex on selection at this scale (Wilk's $\lambda = 0.45$, $F_{[7,9]} = 1.56$, $P = 0.26$). Aspen-dominated deciduous forests were again significantly selected ($t = 2.21$, $P = 0.041$), whereas conifer forest ($t = -3.06$, $P = 0.074$), fields ($t = -2.74$, $P = 0.015$), and human-used land ($t = -4.33$, $P = 0.0005$) were again significantly avoided. But deciduous ($t = 1.12$, $P = 0.28$), mixed ($t = 1.18$, $P = 0.26$), and aspen-dominated mixed ($t = 0.54$, $P = 0.60$) forests were not significantly selected (Fig. 3b). Habitats were ranked as Aspen-D. >>> Decid. > Mixed > Aspen-M. > Field >>> Conif. > Anthro.

Fourth order of selection (no den data set only)

Use of habitat types was not random at this scale (Wilk's $\lambda = 0.31$, $F_{[4,13]} = 7.28$, $P = 0.0026$) and there was no signifi-

cant effect of sex on selection (Wilk's $\lambda = 0.76$, $F_{[4,12]} = 0.95$, $P = 0.47$). Fruit trees were significantly selected ($t = 3.04$, $P = 0.0078$), aspen ($t = 1.88$, $P = 0.079$) and cedar ($t = 0.55$, $P = 0.59$) were selected (although not significantly), and all other deciduous ($t = -2.30$, $P = 0.035$) and conifer ($t = -2.62$, $P = 0.019$) species were significantly avoided (Fig. 4). Species or group of species were ranked as Fruit >>> Aspen > Cedar >>> Decid. > Conif.

Discussion

We first discuss use of dens by porcupines and its influence on the different scales of habitat selection. We then discuss the multi-scale nature of habitat selection by porcupines. Finally, we discuss the variety of constraints that influence habitat selection across scales.

Den use

We identified more than 300 rock dens during our long-term study of the population (2000 and ongoing; D. Berteaux, unpublished data), and most animals changed dens often and used high-quality dens most of the time. Den availability was thus obviously not a limiting factor in our study area.

Porcupines use dens extensively as shelters during winter (Roze 1987; Griesemer et al. 1996; 1998; Zimmerling and Croft 2001) and select rock dens when possible (Griesemer

Fig. 3. Mean proportion of habitat types (Conif., conifer forest; Decid., deciduous forest; Aspen-D., trembling aspen dominated deciduous forest; Field, fields; Anthro., human-used land; Mixed, mixed forest; Aspen-M., trembling aspen dominated mixed forest) in porcupine home ranges (bars indicate habitat availability) against their proportion in used (diamonds) habitat patches for the complete data set (A) and the no den data set (B). Standard errors are shown. Plotted data are population means, but statistics were performed on paired data for each individual. An asterisk indicates statistically significant selection or avoidance ($P < 0.05$).

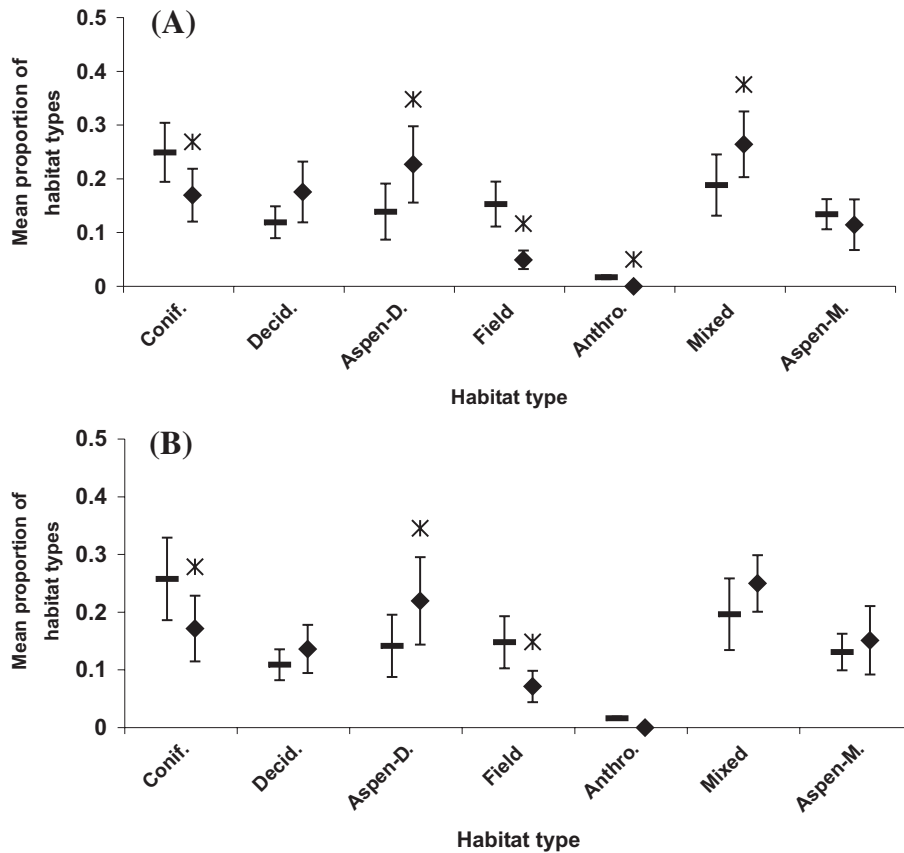
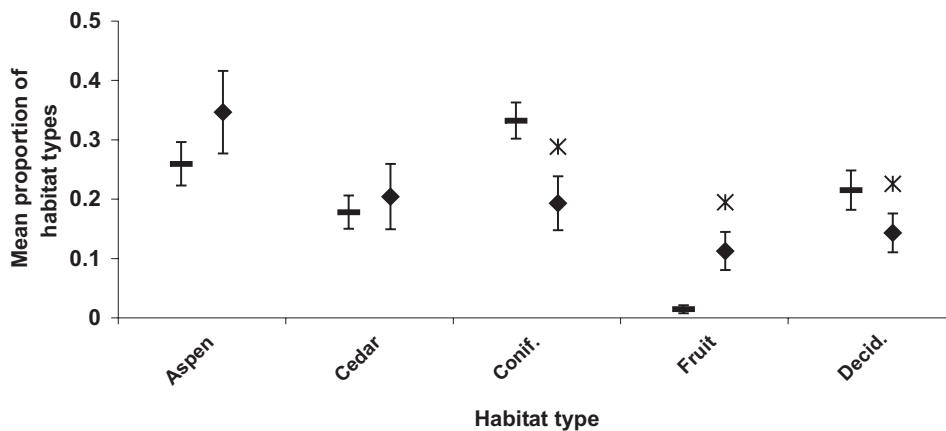


Fig. 4. Mean proportion of habitat type (Aspen, trembling aspen; Cedar, eastern white cedar; Conif., all conifers except Cedar; Fruit, fruit-producing deciduous trees; Decid., all deciduous species except Aspen and Fruit trees) in used habitat polygons (bars indicated habitat availability) against their use (diamonds) by porcupines for the no den data set. Standard errors are shown. Plotted data are population means, but statistics were performed on paired data for each individual. An asterisk indicates statistically significant selection or avoidance ($P < 0.05$).



et al. 1998). We were surprised to see such an intense use of rock dens in summer, because previous studies had shown that porcupines tended to spend the summer in trees (Marshall et al. 1962; Roze 1984; 1987; Griesemer et al. 1996; 1998). The unusual abundance of rock dens in our study

area, coupled with the presence of biting insects and specialized mammalian predators (i.e., fishers, *Martes pennanti* (Erxleben, 1777)), might explain this pattern.

Results obtained from the complete data set and the no den data set were very similar. This indicates that porcupines

did not select habitats according to the presence of dens, as was expected from the large number of high-quality dens present in the study area. Therefore, we can now discuss habitat selection based on vegetation only.

Multi-scale habitat selection

Porcupine usage of habitat was selective at some (but not all) scales, which brings us to compare the three levels of habitat selection and to evaluate the hierarchy among these levels. At the second order of selection, porcupines established home ranges with a habitat composition that was not significantly different from the proportions available within the landscape. The study area as a whole therefore seemed suitable for porcupines, which makes detection of selection patterns difficult at the second order (Aberg et al. 2000).

Selection patterns emerged at the third order of selection. Porcupines choose aspen-dominated deciduous forest and mixed forest. This is not very surprising because aspen is the main food source in their diet (73% of our observations of feeding animals were in aspen, $n = 33$). They seem to prefer getting to aspen where it is dominant, instead of where it is mixed with conifers, a habitat that is used in proportion to its availability. Unexpectedly, they selected mixed forest over aspen-dominated mixed forest, which was contrary to our first impression that aspen-containing habitats should have been selected. Porcupines avoided pure conifer forests, fields, and human-used land. Pure conifer forests lack food in summer, and their avoidance was consistent with the avoidance of conifers other than cedar at the fourth scale. Note that conifer forest and conifer trees are, at all levels, the most available resource category.

We did not take behaviour into account at the fourth order to differentiate between trees that were used for feeding or resting, because in 21% of the observations in trees the observer recorded disturbed porcupine behaviour. Instead of removing these observations from the data set and then using behaviour in our analyses, which could yield biased conclusions, we preferred to use tree observations irrespective of behaviour.

Only some porcupines feed in fields during summer. This restriction in usage of fields is probably why they appear avoided or least selected. Trails and roads are seldom used, but they serve mostly as "highways" in night travelling as we regularly observed. The chance of tracking an individual down using telemetry at the exact moment where it is walking on a trail is extremely low, which is why this habitat is one of the most avoided.

The fourth order of selection showed that fruit trees were important to porcupines, especially males. We used the ripening of fruits of mountain ash to determine the end of the "porcupine summer", focussing on the summer diet. Hence, this result was unexpected. Perhaps some animals were anticipating the ripening of fruits of mountain ash in late August and eating the leaves while visiting the trees, which would explain the importance of fruit trees to porcupine.

The no den data set confirmed also that aspen alone was relatively important for porcupines, especially females, even though it was so widespread in our study area. As a consequence of this nearly monospecific diet, all other species of deciduous trees were ranked lower. Because eastern white cedar is the favoured resting tree species of porcupines, it

makes sense that other conifers were used less than they were available.

Most research on porcupine habitat use considered solely the tree level (fourth order of selection) (e.g., Marshall et al. 1962; Gill and Cordes 1972; Harder 1980; Roze 1987; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001), but comparison of our results with these is difficult because most concern winter use.

The no den data set allows us to compare and contrast results obtained at all three scales. Porcupines consistently avoided human-used land at the second and third orders. But this is the only common point between results at the second and third orders. Between the third and fourth orders, the selection of aspen and avoidance of conifer forest were consistent. The three categories of deciduous species that we used at the fourth order allowed us to understand porcupine habitat use better than we could have at the third order. Consequently, we were able to detect the strong selection of fruit-producing trees, the selection of aspen, and the avoidance of all other deciduous species. These patterns differed from previous reports of porcupine habitat selection because the available tree species were different. In these studies, a great deal of attention was given to tree species selection (Griesemer et al. 1998; Zimmerling and Croft 2001), with little effort on how it translated at lower orders of selection (home-range scale or landscape scale) as we have done here.

Our results concur with many studies of porcupine habitat selection and arbicolous folivores in general, which show that porcupines do not feed on tree species at random (Gill and Cordes 1972; Roze 1984; Sullivan et al. 1986; Snyder and Linhart 1997; Griesemer et al. 1998; Zimmerling and Croft 2001). There is a great level of variation in the feeding ecology of arboreal folivores (Lawler et al. 1998). The chemical composition, nutritional quality, and plant secondary metabolites of foliage are brought forward as potential explanations to the observed foraging behaviour in arbicolous folivores (Roze 1989; Snyder and Linhart 1997; Lawler et al. 1998; McIlwee et al. 2001).

Conclusion

Our results confirm the need to adopt a multi-scale approach in habitat-selection studies, because habitat selection is not necessarily congruent across scales (Chamberlain et al. 2002; McLoughlin et al. 2002). Conclusions at one scale may not apply to all scales (Wiens 1989). Rettie and McLoughlin (1999) proposed that decisions at coarser scales should reveal environmental features which are more important to fitness than decisions at finer scales. In our porcupine population, significant patterns of habitat selection emerged from the third and fourth orders, but not from the second order. The absence of selection patterns at the second order could mean that (i) porcupines are not faced with significant limiting factors at this scale, (ii) our study area is already more suitable than the surroundings and some selection occurred at an even coarser scale, or (iii) densities are so high that subordinate individuals are forced to use suboptimal habitats.

We found that porcupines are generalists at the second order, and that third and fourth orders better describe the needs of these herbivores. Our results thus echo those of Fortin et al. (2003) who suggested that "the link between selection of

forage and habitat seemed to weaken as non-foraging constraints increased in importance at larger scales". Future research should now attempt to identify these non-foraging constraints.

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