Journal of Mammalogy, 95(5):992–1003, 2014

Hide or die: use of cover decreases predation risk in juvenile North American porcupines

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In many mammals, juveniles are vulnerable to predators because of their low mobility and small body size. Cover hides juveniles from predators and has been assumed to lower predation risk. However, among mammal species, studies relating use of cover to fitness remain infrequent and have been predominantly performed on ungulates. We measured habitat selection and survival of juvenile North American porcupines (*Erethizon dorsatum*). We tested whether juveniles selected for cover, use of cover depended on meteorological conditions (there could be a trade-off between predation risk and radiative heat gain during sunny days), and use of cover influenced survival. We also examined how sex, body mass, mobility of the juvenile, and distance to the mother affected survival. We found that juvenile porcupines (14 individuals observed on 299 occasions) selected high protective cover (microhabitat scale) within areas with low herb cover (local scale). Use of cover partly depended on weather, with use of dens decreasing on sunny and warm days but use of cover outside of the den being independent of meteorological conditions. Ten juveniles died during the study and 90% of deaths were due to predation. Use of microhabitats with high protective cover and use of sites with high shrub cover at the local scale enhanced survival. We found no effect on survival of sex, body mass, mobility, and distance to the mother. These results demonstrate that use of cover was crucial to survival in a system where predation was the main limiting factor, and that predation risk was modulated by habitat use of juveniles.

Key words: conditional logistic regression, hider, predation, thermoregulation

DOI: 10.1644/13-MAMM-A-308

In many vertebrates, juvenile survival is more sensitive to environmental variation than is adult survival (Gaillard et al. 2000; Eberhardt 2002; Gaillard and Yoccoz 2003). Juvenile survival can play a fundamental role in driving the dynamics of populations (Coulson et al. 1997; Gaillard et al. 2000), and thus identifying the causes of variation in early survival constitutes an important issue in evolutionary ecology, population management, and conservation (see Linnell et al. [1995] and Gaillard et al. [1998, 2000] for reviews). One reason why juvenile survival is highly variable may have to do with juveniles' vulnerability to predation, caused by their small size, low mobility, and lack of experience (Molinari-Jobin et al. 2004; Hoogland et al. 2006).

Newborn mammals are often categorized as followers or hiders depending on their antipredatory strategy (Lent 1974). In species where juveniles follow their mother, mothers minimize predation risk to their offspring by using habitats with fewer predators or greater opportunities to evade predation (Bleich et al. 1997; Rachlow and Bowyer 1998; Panzacchi et al. 2010). For species relying on hiding behavior, characteristics of the hiding site may determine the level of protection from predators. Still, studies relating characteristics of the hiding site to juvenile survival are uncommon and largely centered on ungulates (see Grovenburg et al. [2012] and Kjellander et al. [2012] for some recent examples). Because diverse constraints may be at play for prey species of varying body size or exposed to different predator communities, we need more studies examining this habitat–fitness relationship, and on a large variety of taxa.

Ungulate fawns select hiding sites providing large amounts of horizontal cover (see review in Mysterud and Ostbye [1999]). This could lower the risk of predation, either by reducing the probability of being detected or through obstruction from attacks (see Gorini et al. [2012] for a review).

Simultaneously, use of cover modulates solar radiation gains and losses (Demarchi and Bunnell 1993), and some large mammals have been shown to use vertical cover during summer to reduce heat stress (e.g., Dussault et al. 2004; van Beest et al. 2012). Neonates, on the other hand, can be sensitive to hypothermia (Gilbert and Raedeke 2004; Olson et al. 2005; Grovenburg et al. 2012) and could thus suffer a fitness cost when utilizing covered habitats because cover impedes access to radiative heat gain (Bowyer et al. 1998). There is thus a potential trade-off between the risk of predation and the risk of hypothermia in juvenile mammals (especially those inhabiting northern or high-altitude environments).

We studied the North American porcupine (*Erethizon dorsatum*), a medium-sized mammal that relies on a hiding antipredatory strategy (Roze 2009), to investigate how the use of cover influenced summer survival of juveniles. Porcupines weigh about 400 g at birth (Roze 2009), remain hidden, and rely exclusively on their mother for food for their first 2–3 weeks of life (Farrell and Christian 1987). They start searching for food after 3 weeks but continue to receive milk from their mother until 70–80 days old. They are potentially exposed to both predation and hypothermia in the northernmost parts of their distribution. Potential predators of juvenile porcupines include great horned owls (*Bubo virginianus*), Canadian lynx (*Lynx canadensis*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray wolves (*Canis lupus*), wolverines (*Gulo gulo*), mountain lions (*Puma concolor*), and fishers (*Martes pennanti*—Roze 2009). Coyotes, great horned owls, and fishers were all regularly observed in our study area (with fishers being the main porcupine predator—Mabille et al. 2010), exposing juveniles to a significant predation risk. Juvenile porcupines are born in mid-May when air temperature at our southern boreal study site can still be as low as 0°C. We thus expected juvenile porcupines to potentially face a trade-off between using cover to decrease predation risk and avoiding cover to increase solar heat gain. We worked at 2 spatial scales (microhabitat [1 m] and local [15 m]) relevant to the ecology of stationary or little-moving juvenile porcupines, and tested the following predictions:

1) Selection for cover occurs at both spatial scales because juvenile porcupines are highly vulnerable to predation (Sweitzer and Berger 1992);
2) Use of cover is dependent on meteorological conditions and should be lower on days when radiative gains are possible (i.e., on sunny days) and, within sunny days, on days when air temperature is the lowest. Even though we predicted avoidance of predators to be the main factor driving habitat selection by juveniles, we expected risk of hypothermia to be high on cold days and therefore to influence habitat use on those days. Juvenile porcupines are poorly insulated (Haim et al. 1992) and may be faced with relatively low temperatures during their 1st weeks of life. We therefore expected them to trade protection from predators against access to radiative heat gain by using open habitats on sunny (i.e., with $\leq 75\%$ of cloud cover) but cold days;
3) If individual differences exist in the use of cover, these may translate into variations in survival. Because predation rates were substantial in our population, leading to a large decline of our study population (Mabille et al. 2010), we expected high use of cover to enhance survival.

Factors other than habitat use can affect survival, either directly or through an increased vulnerability to predation. Therefore, we did not separate our tests from their ecological context and used our data to also ask whether sex (Aanes and Andersen 1996; May et al. 2008); body mass on 10 June, used as indicator of relative date of birth (Keech et al. 2000; Côté and Festa-Bianchet 2001); mobility (Norrdahl and Korpimaki 1998; Yoder et al. 2004; Piccolo et al. 2010); and distance between a juvenile and its mother (Mathisen et al. 2003) influenced summer survival of juveniles.

MATERIALS AND METHODS

Study Area and Study Population

We worked from 1 May to 15 August (2003 and 2004) in the Parc National du Bic (48°20′N, 68°46′W, elevation 0–150 m), Quebec, Canada. The study area is characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest dominated by quaking aspen (*Populus tremuloides*, hereafter called aspen), eastern white cedar (*Thuja occidentalis*, hereafter called cedar), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*). The area is fragmented by abandoned and cultivated fields where porcupines feed during the snow-free period and are easily captured (Morin et al. 2005). At the beginning of spring, we captured and chemically immobilized (Morin and Berteaux 2003) adult females to fit them with very-high-frequency (VHF) transmitters (SMRC-5RB; Lotek Wireless Inc., Newmarket, Ontario, Canada). Capture techniques and immobilization procedures followed guidelines of the American Society of Mammalogists (Sikes et al. 2011) and were approved by the Université du Quebec à Rimouski Animal Care Committee (protocol project N° CPA 12-02-06) and the Société de la Faune et des Parcs, Gouvernement du Quebec (permits 20000417-001-01-S-P to 20060501-002-01-S-F). We used the VHF transmitters to regularly locate females and search for juveniles ($>$ 240 h of search) near lactating females. We found 10 juveniles in 2003 and 4 in 2004, fitted them with VHF transmitters (R1-2DM, 7.5 g; Holohil Systems Ltd., Carp, Ontario, Canada) and subsequently followed their habitat use until 15 August. We located juveniles 5 days a week by following the signal of the animal (homing; see Morin et al. [2005] for details), and recorded their location using a handheld global positioning system. When approaching juveniles, we carefully listened for any changes in signal regularity and for noises in the woods to determine whether the approached juvenile was moving or not. We removed from analyses the few instances ($n = 8$) when juveniles were changing location during our approach. Our telemetry effort was concentrated in the daytime, with 90% of locations obtained between 9 AM and 5 PM. We distributed sampling along the diurnal cycle evenly across individuals.

Habitat Selection

Each time we located a still, undisturbed animal ($n = 299$ observations), we recorded where the animal was hiding (in a den, on the ground, or in a tree—Comtois and Berteaux 2005) and then characterized the habitat at the hiding site and at a paired random site (20 m away but at the same height as the animal location, following a randomly determined compass heading). If the porcupine was in a tree, the random site was chosen in the nearest tree 20 m away from the hiding site, and the characteristics of the hiding and random sites were estimated at the height where the animal was situated (e.g., at 10-m height). We recorded the percentage of protective cover at the microhabitat scale (cover provided by rocks, trees, and foliage, visually estimated as < 25%, 25–50%, 51–75%, or > 75% within a 1-m-radius circle centered on the hiding or random site), and the vegetation characteristics at the local scale (within 15 m of the hiding or random site). The vegetation characteristics measured were the dominant tree species and the percentages of tree, shrub (woody vegetation between 50 and 150 cm tall), and herb (nonwoody vegetation) cover in a 15-m-radius circle centered on the site of interest (cover visually estimated as < 25%, 25–50%, 51–75%, or > 75%). The dominant tree species was characterized as aspen, fruit-bearing trees (serviceberry [*Amelanchier* sp.], American mountain-ash [*Sorbus americana*], and pin cherry [*Prunus pensylvanica*]), other deciduous trees, cedar, or other coniferous trees (white spruce or balsam fir). Because the random site was located only 20 m from the animal, the vegetation characteristics of the hiding and random sites were not independent (approximately 22% surface overlap between the 2 areas considered for estimation) and this decreased the likelihood of detecting differences between the 2 sites. Our tests of selection at the local scale were therefore conservative.

Effects of Meteorological Conditions on the Use of Cover

We measured air temperature (°C) and recorded whether the day was generally sunny ($\leq$ 75% of cloud cover) or not (> 75% of cloud cover) each time we located a porcupine. We tested whether the use of dens or protective cover (when outside of a den) was dependent on sunny days and, for sunny days, whether the use of dens or protective cover was dependent on air temperature.

Individual Indicators of Habitat Use

We first compiled individual indicators of habitat use for descriptive purposes. We determined the percentage of times a juvenile was in a den, on the ground, or in a tree, and calculated the mean percentage of protective cover experienced by each individual at the microhabitat scale (assigning values of 25%, 50%, 75%, and 100% of cover to observations that fell respectively in categories < 25%, 25–50%, 51–75%, and > 75% of cover during the visual evaluation). At the local scale, we calculated the mean tree, shrub, and herb cover present in sites used by each individual (using approximations described above). Second, we used those estimates compiled at the individual level to test whether juveniles differed in their use of cover (at both scales) as well as in their use of den, ground, and tree locations (see statistical analyses). Finally, when juveniles showed significant individual differences in use for a given variable, we tested whether habitat use with respect to this variable influenced survival.

Sex, Body Mass on 10 June, Mobility, and Distance to the Mother

We sexed juveniles by palpating the genital area (Dodge 1982) and weighed them once a week from the date they were first captured to 15 August. We used body mass on 10 June as an indicator of relative date of birth. We chose 10 June because all juveniles were born on or before that date (range of birth dates: 6 May–10 June), and because we measured body mass for 10 of 14 juveniles on that date. For the remaining 4 individuals, we estimated body mass on 10 June by adding or removing 30 g/day (average daily mass gain in June calculated over all individuals) from the body mass measured on the day closest to 10 June (27 May, 1 June, 1 July, and 6 July). We characterized the mobility of juveniles using the mean distance they moved in a day (calculating the distance travelled as a straight line between locations separated by 1 day only). Finally, when we knew the identity of the mother ($n = 11$), we located it twice a week, just before or after locating its juvenile, in order to calculate the distance between mother and juvenile (in meters). We calculated mean daily movements of juveniles and mean distance to the mother separately for May, June, July, and August (for descriptive purposes), but used overall mean daily movements and overall mean distance to the mother in survival analyses.

Survival

We calculated survival time as the time from birth to death (exact time; 10 juveniles) or from birth to the end of the study period when individuals remained alive (15 August, censored time; 4 juveniles). We estimated date of birth from mass at 1st capture assuming a mean mass gain of 30 g/day (see above). When we found a dead juvenile, we determined cause of mortality as starvation (not injured, intact carcass), predator killed (traces of blood on radiocollar or wounds on the carcass), or unknown.

Statistical Analyses

Habitat selection (prediction 1).—We built models of habitat selection by comparing used and random sites to obtain resource selection functions (Manly et al. 2002). Resource selection functions are equations that predict the relative probability of use, taking the form:

$$\mathrm{w(x)} = \mathrm{e}(\beta_1 \mathrm{x}_1 + \beta_2 \mathrm{x}_2 + \ldots + \beta_n \mathrm{x}_n), \qquad (1)$$

where w(x) is the resource selection function value, e is the base of the natural logarithm, β_is are the estimated coefficients, and x_is are habitat variables. We used matched case–control or

Table 1.—Use of cover by juvenile North American porcupines (*Erethizon dorsatum*) at the microhabitat (1 m) and local (15 m) scales in Parc National du Bic, Quebec, Canada, May–August, 2003–2004. Results are reported as the mean for each individual (A–N) and the population (calculated from individual means). Levels of significance for between-individual differences in habitat use are indicated as * $P < 0.05$, ** $P < 0.01$, and *** $P < 0.001$.

	A	B	C	D	E	F	G	H	I	J	K	L	M	N	$\bar{X}$
Observations (*n*)	5	3	46	13	33	3	18	8	30	47	38	2	28	25	21
Survival time (days)	22	30	87[a]	31	67	27	37	29	66	101[a]	83	23	71[a]	73[a]	53
Microhabitat scale															
Protective cover*** (%)	63	42	69	88	65	75	88	84	77	77	82	63	90	87	75
Use of den** (%)	40	0	28	46	40	67	67	75	53	43	45	0	82	76	47
Use of ground* (%)	20	33	13	54	33	33	17	13	27	13	39	50	4	8	26
Use of tree*** (%)	40	67	59	0	27	0	16	12	20	44	16	50	14	16	27
Local scale															
Tree cover*** (%)	70	75	65	54	63	50	49	97	58	62	67	75	84	67	67
Shrub cover*** (%)	25	25	41	27	38	33	56	25	33	38	38	25	33	32	34
Herb cover* (%)	25	33	33	25	26	58	33	28	38	39	32	25	29	27	32

[a] Survival time is censored (i.e., individual was still alive on 15 August).

conditional logistic regression (Hosmer and Lemeshow 1989) to estimate coefficients. Each pair of used–random points was defined as a stratum in analyses so that conditional logistic regression compared use with availability in a given pair, which is particularly adapted to studies of microhabitat or microclimate selection, or both (Compton et al. 2002).

Because the number of observations was low for some animals ($\bar{X} \pm SE = 21 \pm 4$ observations, range = 2–47 observations; Table 1), we could not determine habitat selection for each individual. Rather, we determined habitat selection for the population, taking into account the pseudoreplication in our analyses (following Fortin et al. [2005], see below). Pseudoreplication does not influence coefficient estimates (β-values), but biases their standard errors (Nielson et al. 2002). We used a robust sandwich estimate of the covariance matrix (Lin and Wei 1989; Wei et al. 1989) to obtain robust standard errors of coefficients. For that we defined all observations coming from a given individual as a cluster and pairs of used–random points as a stratum, and analyzed our data using SAS software, proc PHREG, version 9.1 (SAS Institute Inc. 2004) following Fortin et al. (2005). Each estimated coefficient is interpreted as usual for logistic regression: a 1-unit increase in an explanatory variable results in a $e^{\beta i}$ increase in the odds ratio. For low-probability events (such as the presence of a juvenile porcupine), the odds ratio approximates the relative risk, that is, the ratio of the probability of event x (e.g., a porcupine being present) given A to the probability of x given B (Hosmer and Lemeshow 1989; Compton et al. 2002). Because we used a Cox proportional hazards model for regression analyses (also used for survival analyses, see below), we show hazard ratios instead of typical odds ratios. However, interpretation of a hazard ratio is similar to that of an odds ratio.

Effects of meteorological conditions on the use of cover (prediction 2).—Because the Julian date influenced both the use of protective cover at the microhabitat scale and the use of dens (juveniles tended to use less cover and use dens less often as they aged, results not shown), we included Julian date in models examining the effects of meteorological conditions on the use of protective cover. Our data set included repeated measurements made on the same individuals at different dates, so we fitted mixed-effect models with porcupine identity as a random factor. We used SAS software, version 9.1 (SAS Institute Inc. 2004) to analyze the effect of meteorological conditions on den use (treated as a binary variable: inside–outside den; proc GLIMMIX) and on the percentage of protective cover used when outside of a den (treated as a continuous variable: 1–4 depending on cover being in class < 25%, 25–50%, 51–75% or > 75%; proc MIXED).

Individual indicators of habitat use (prediction 3).—We tested for individual differences in habitat use using all observations ($n = 299$) and general linear models in SAS software version 9.1 (SAS Institute Inc. 2004). We used identity of juveniles as the explanatory variable in all analyses and amount of protective cover; amount of tree, shrub, and herb cover (continuous variables; proc GLM); or use of a den, ground, and tree location (binary variables; proc LOGISTIC) as dependent variables.

Survival (prediction 3).—We analyzed juvenile survival using a Cox proportional hazards model (Cox 1972). In the proportional hazards model, the cumulative survival function S(*t*), which defines the probability of surviving longer than time *t* (here expressed in days), is expressed as a hazard function, which is the derivative of the survivor function over time (i.e., instantaneous probability of death):

$$\mathrm{h}(t) = d\mathrm{S}(t)/dt. \tag{2}$$

The proportional hazards model is:

$$\mathrm{h}(t) = \mathrm{h}_0(t)\mathrm{e}\left[\beta_1 \mathrm{x}_1 + \beta_2 \mathrm{x}_2 + \ldots + \beta_\mathrm{p} \mathrm{x}_\mathrm{p}\right], \tag{3}$$

where $\mathrm{h}_0(t)$ is the baseline hazard function, e is the base of the natural logarithm, β_is are regression coefficients, and x_is are model covariates. We wanted our covariates to describe the habitat use of each juvenile porcupine as well as its sex, mass on 10 June, mobility, and mean distance to the mother. We used proc PHREG in SAS software version 9.1 (SAS Institute

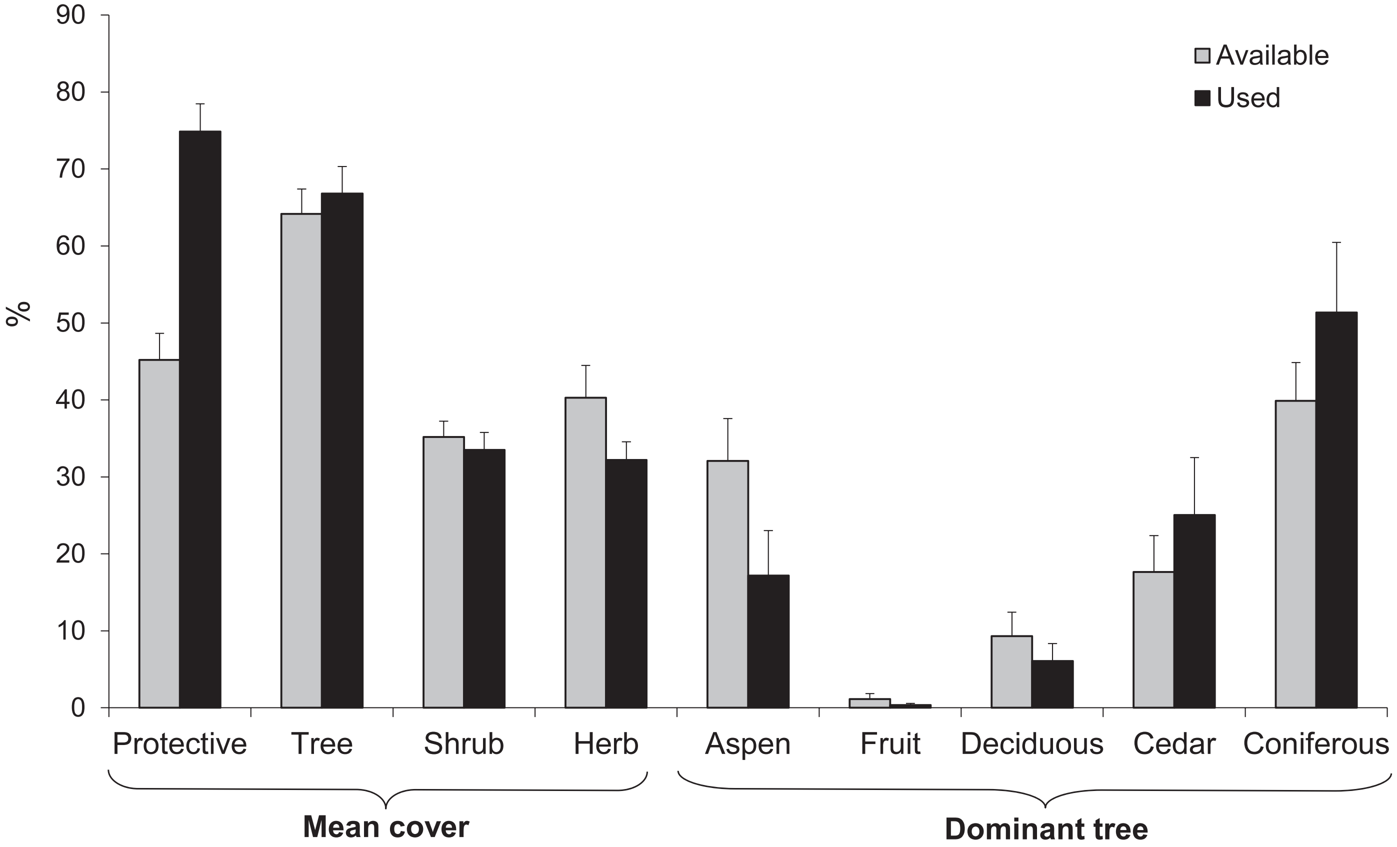

FIG. 1.—Characteristics of hiding sites used by 14 juvenile North American porcupines (*Erethizon dorsatum*), and available random sites in Parc National du Bic, Quebec, Canada, May–August, 2003–2004. Results shown are means (± *SE*) for the population (calculated from individual means, $n = 14$ individuals on which were performed 299 observations). Percentage of protective cover at the microhabitat scale (1 m); percentage of tree, shrub, and herb cover at the local scale (15 m); and mean percentage of occurrences when the dominant tree species was an aspen, fruit-bearing, other deciduous, cedar, or other coniferous tree.

Inc. 2004) to examine how these different covariates were associated with survival time. Because we collected data from only 14 juveniles, we did not have the power to examine in a given model the effect of several explanatory variables. We thus ran separate analyses to examine in univariate models if variables describing use at the microhabitat scale (i.e., amount of protective cover used; and use of den, tree, and ground locations), variables describing use at the local scale (i.e., tree, shrub, and herb cover in the site), and individual characteristics (i.e., sex, body mass on 10 June, mobility of the juvenile, and distance to the mother) influenced survival. A preliminary analysis of cover type usage found that the use of protective cover at the microhabitat scale and use of dens tended to decrease while the use of trees and ground locations tended to increase as juveniles aged. Therefore, we used residuals for these variables to test for influences on juvenile survivorship.

RESULTS

Habitat selection.—Juveniles selected hiding sites characterized by a high protective cover (Fig. 1; Table 2). The hazard ratio allowed us to quantify selection for cover, and indicated that a 25% increase in protective cover was associated with a 413% increase in selection. At the local scale, juveniles selected areas with low herb cover and with cedar as dominant tree species (Fig. 1; Table 2). The hazard ratios indicated that a 25% increase in herb cover was associated with a 40% decrease in selection and that the presence of cedar as dominant tree species was associated with a 147% increase in selection compared to when aspen was dominant (Table 2).

Effects of meteorological conditions on the use of cover.—Den use decreased on sunny days (–0.616 ± *SE* 0.232, $F_{1,283} = 7.07$, $P = 0.008$; Fig. 2) and, during sunny days, decreased with increasing temperature (–0.126 ± 0.049, $F_{1,141} = 6.61$, $P = 0.011$; Fig. 2). On the other hand, use of protective cover outside of the den was neither influenced by the day being sunny or overcast (0.016 ± 0.159, $F_{1,134} = 0.01$, $P = 0.92$; Fig. 2) nor by the air temperature during sunny days (0.021 ± 0.031, $F_{1,71} = 0.47$, $P = 0.49$; Fig. 2).

Individual indicators of habitat use.—We found juveniles inside dens, on the ground, and in a tree 47%, 26%, and 27% of the times, respectively, that we located them. Individuals significantly differed in their use of den, tree, and ground locations (Table 1). On average, juveniles used microhabitats

Table 2.—Coefficients for the resource selection functions at the microhabitat (1 m) and local (15 m) scales for hiding sites used by 14 juvenile North American porcupines (*Erethizon dorsatum*) in Parc National du Bic, Quebec, Canada, May–August, 2003–2004. ND = non-defined.

Variable	β-value	Robust *SE*	χ^2	*P*	Hazard ratio
Microhabitat scale					
Percent cover	1.635	0.144	128.7	< 0.001	5.13 (25%)
Local scale					
Tree cover	–0.101	0.226	0.20	0.65	0.90 (25%)
Shrub cover	–0.151	0.177	0.73	0.39	0.86 (25%)
Herb cover	–0.509	0.233	4.76	0.029	0.60 (25%)
Dominant tree					
Aspen	0	ND	ND	ND	Reference category
Fruit-bearing	–0.742	1.460	0.26	0.61	0.48
Other deciduous	0.274	0.435	0.40	0.53	1.32
Cedar	0.904	0.278	10.6	0.001	2.47
Other coniferous	0.465	0.271	2.94	0.087	1.59

providing 75% of protective cover but individuals significantly differed in the mean protective cover they used (Table 1).

At the local scale, juveniles used sites with an average of 67% tree cover, 34% shrub cover, and 32% herb cover but individuals significantly differed in the mean tree, shrub, and herb cover they used (Table 1). The amount of tree cover was negatively correlated to the amount of shrub (Spearman rank correlation, $r = -0.22$, $P < 0.001$, $n = 299$) and herb cover (Spearman rank correlation, $r = -0.21$, $P < 0.001$, $n = 299$) present at the site.

Sex, body mass, mobility, and distance to the mother.—Eight of the studied juveniles were females and 6 were males. Mean body mass on 10 June was 930 ± *SE* 96 g (range: 350–1380 g, $n = 14$), and was not different between sexes ($F_{1,12} = 0.05$, $P = 0.82$). Mean daily length of movement varied through time ($F_{3,12} = 4.91$, $P = 0.019$) with shorter distances moved in May and June compared to July and August (Table 3) but was not different between sexes ($F_{1,11} = 0.04$, $P = 0.84$). Mean distance between juvenile and mother also varied through time ($F_{3,8} = 8.17$, $P = 0.008$) with shorter distances

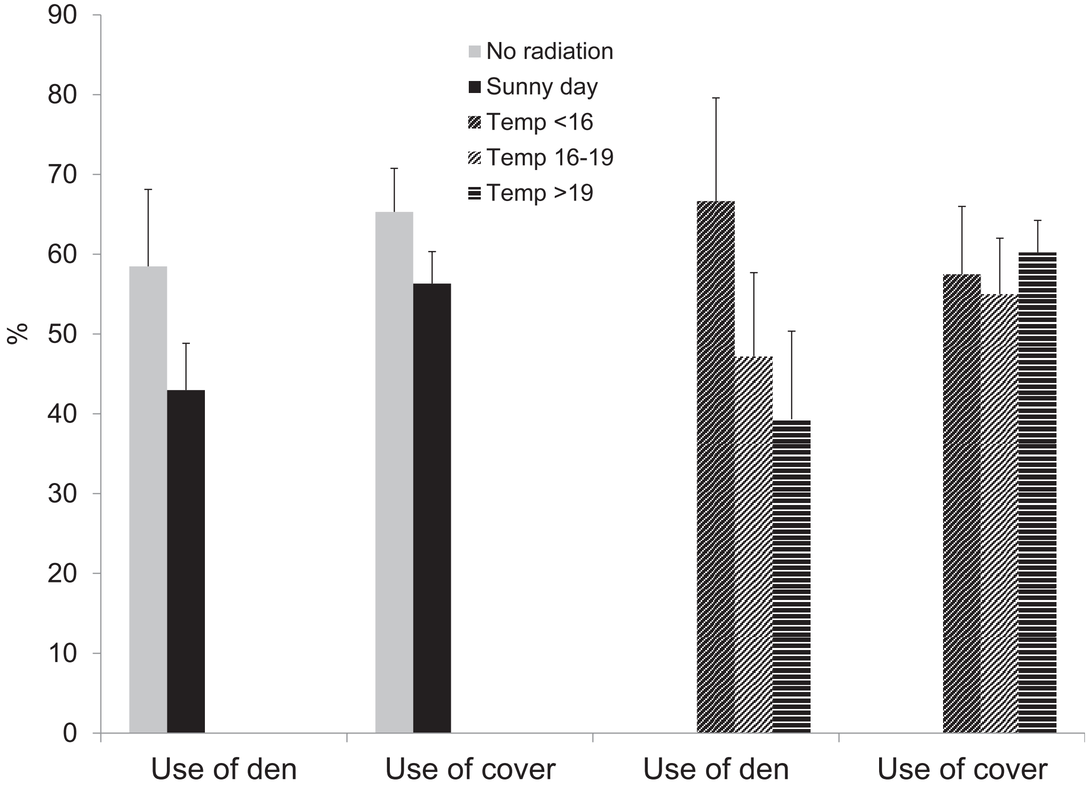

Fig. 2.—Use of den (% of animal locations) and use of protective cover at the microhabitat scale (% cover within 1 m of the animal, when outside of the den) as a function of meteorological conditions: radiation (no radiation versus sunny day) and, for sunny days, as a function of air temperature (°C) for 14 juvenile North American porcupines in Parc National du Bic, Quebec, Canada, May–August, 2003–2004.

TABLE 3.—Length of daily movements (m) and distance from mother (m) for juvenile North American porcupines (*Erethizon dorsatum*) followed in Parc National du Bic, Quebec, Canada, May–August, 2003–2004. Means (± *SE*) for the population (calculated from individual means) are given by month and for the study period. The range of individual means and the sample sizes (number of individuals, number of observations) also are given.

	May	June	July	August	Overall
Daily movements					
$\bar{X} \pm SE$	9 ± 3	47 ± 8	77 ± 15	70 ± 23	54 ± 8
Range	3–24	17–83	40–149	26–134	17–102
n	7, 11	9, 102	8, 89	4, 23	13, 225
Distance to the mother					
$\bar{X} \pm SE$	15 ± 9	99 ± 19	171 ± 52	135 ± 125	96 ± 21
Range	5–33	24–201	48–380	7–384	24–236
n	3, 5	10, 60	6, 39	3, 14	11, 118

between mother and young in May compared to other months (Table 3) but was not different between sexes ($F_{1,9} = 0.15$, $P = 0.71$).

Survival.—Nine of the 10 observed deaths were due to predation and 1 juvenile died of unknown cause. Most of the predation events were probably due to fishers because we found small teeth marks on several collars worn by killed juveniles. We also photo-trapped a fisher next to one of the killed juveniles. The youngest juvenile to die was 22 days old, whereas the oldest juvenile observed alive was aged approximately 101 days when the study ended (Table 1). Habitat use at the microhabitat and local scales influenced survival of juveniles. At the microhabitat scale, use of high protective cover enhanced survival (a 25% increase in the mean protective cover used was associated with a 68% decrease in death probability [Table 4]). At the local scale, and although the effect was only marginally statistically significant, use of sites with higher shrub cover increased survival (Table 4). According to the hazard ratio, a 25% increase in mean shrub cover used was associated with a 98% decrease in death probability. We found no effect of sex ($\chi^2_1 = 0.30$, $P = 0.59$), mass on 10 June ($\chi^2_1 = 0.01$, $P = 0.92$), mobility ($\chi^2_1 = 1.22$, $P = 0.27$), or distance to the mother ($\chi^2_1 = 0.32$, $P = 0.57$) on survival.

DISCUSSION

We now discuss our findings to evaluate our 3 original predictions.

Habitat selection.—In species relying on hiding behavior to escape predators, the mother leads her young to a bedding area where the young selects a bed site (Huegel et al. 1986; Alldredge et al. 1991). In this study, mothers were therefore probably responsible for habitat selection measured at the local scale, whereas juveniles likely selected microhabitat. We predicted selection for cover to occur at both scales (prediction 1) because juvenile porcupines were found by Sweitzer and Berger (1992) to avoid open areas in presence of predators, and because predation risk was high in our study site (Mabille et al. 2010). Mothers thus probably selected stands offering the best possible protection to their young (Bongi et al. 2008; Van Moorter et al. 2009; Leclerc et al. 2012). Our study animals selected microhabitats with high protective cover within habitat patches showing low herb cover and dominated by cedar trees. We could not detect selection for high tree or shrub cover (at the local scale), even though stands with low herb cover were typically dense in our study area, as illustrated by the negative relationship we found between tree and herb cover. We may have lacked the power to detect selection at the local scale because we had some surface overlap between the 2 areas considered for evaluation of the vegetation characteristics

TABLE 4.—Coefficients for the survival analyses for 14 juvenile North American porcupines (*Erethizon dorsatum*) studied in Parc National du Bic, Quebec, Canada, May–August, 2003–2004. Results were obtained from 7 univariate models (i.e., each variable was examined in its own model, separately from the other variables).

Variable	β-value	*SE*	χ^2	*P*	Hazard ratio
Microhabitat scale					
1—Protective cover	−1.141	0.534	4.55	0.033	0.32 (25%)
2—Use of den	−0.507	0.342	2.19	0.14	0.60
3—Use of ground	0.560	0.427	1.72	0.19	1.75
4—Use of tree	0.372	0.256	2.12	0.15	1.45
Local scale					
5—Tree cover	−0.570	0.813	0.49	0.48	0.57 (25%)
6—Shrub cover	−3.787	2.001	3.58	0.058	0.02 (25%)
7—Herb cover	0.607	1.208	0.25	0.62	1.84 (25%)

at the local scale (see "Materials and Methods"). We suggest that some selection for high tree cover occurred at the landscape scale (not investigated in this study) because we always located juveniles in forested environments, whereas our study area was fragmented by open fields used by adult porcupines for feeding (Morin et al. 2005; this study). Open areas therefore constituted exploitable areas for adults but were not used by juveniles.

Our results support the hypothesis that predator avoidance was the main factor driving habitat selection at the 2 scales studied. Indeed, use of covered microhabitats is likely to decrease probability of detection by predators (Mysterud and Ostbye 1999), whereas use of areas with low herb cover should reduce the likelihood of encountering predators. Indeed, herb cover in forested environments is mainly associated with open or edge habitats, which are easily accessible to predators and used by many of them for hunting (Salek et al. 2010; Cervinka et al. 2011; Rearden et al. 2011). According to Rettie and Messier (2000, p. 467), "a limiting factor should continue to dominate selective behavior at successively finer scales until it becomes less important than the next most important limiting factor." Predation therefore appeared to be a very important limiting factor for juvenile porcupines because predator avoidance dominated habitat selection by the young and the mother up to the microhabitat scale. Previous studies have shown that forage availability was limiting at the home-range level for mothers, who thus had to trade access to forage against safety of their young (e.g., Panzacchi et al. 2010; Rearden et al. 2011). In mixed and boreal forests, porcupines are the only arboreal folivorous mammal (Roze 2009), so forage availability may not be limited by competition and this may explain why access to forage was not an important driver of habitat selection.

Effects of meteorological conditions on the use of cover.—In summer, use of cover by animals usually results in a lower access to incoming radiation and thus in exposure to lower temperatures (e.g., Allred et al. 2013; Scheffers et al. 2014). We therefore expected juvenile porcupines to use open environments on sunny and cold days in order to maximize radiative heat gain (prediction 2). Results did not support this prediction, however, despite cold temperatures occurring in our study area, especially in May when the young were the most sensitive to hypothermia (average minimum temperature in May registered at the Rimouski weather station, approximately 25 km from our study area, was 4.7°C and 3.9°C in 2003 and 2004, respectively). Juvenile porcupines rather increased their use of dens when temperature decreased, even on sunny days. We presume juveniles were able to warm their dens when using them so that dens constituted unique covered microhabitats that provided shelter against cold temperatures. Juveniles thus used dens as thermal refuges and mainly exited their dens when the outside thermal environment was mild. Juveniles therefore did not appear to face a trade-off between use of cover and thermal exposure, but rather a trade-off between benefiting from thermal protection in dens and acquiring food, because dens provided no foraging opportunities.

Outside the den, we found no effect of meteorological conditions on the use of protective cover. This pattern contradicts our 2nd prediction, and suggests that cover outside the den was used as hiding cover, with juveniles retreating to dens when temperature decreased. Behavioral thermoregulation of North American porcupines during the winter also is based on using dens as thermal refuges, whereas outside microhabitats are chosen according to the foraging opportunities they can provide in a season when food is limited (Mabille et al. 2011). The possibility of using dens, which provide a stable and predictable thermal environment (Campos et al. 2013), seems to free porcupines from the constraint to select microhabitats with elevated light penetration (Van Moorter et al. 2009), thus allowing them to concentrate on hiding. Hiding, even when outside of the den, thus seemed to be the most important limiting factor for juvenile porcupines that receive food from their mother but are very vulnerable to predation (Lingle et al. 2008).

Habitat use and survival.—Predation was the main cause of mortality in juvenile porcupines. Several predators hunt and kill porcupines more effectively in open habitats (coyotes [Keller 1935], mountain lions [Robinette et al. 1959], and fishers [Powell and Brander 1977]) and porcupines perceive open habitats as risky habitats (Sweitzer and Berger 1992). Consistent with the hypothesis that open habitats are more risky, we found that use of cover (both at the microhabitat and local scales) enhanced survival. There were individual differences in the use of cover and juveniles survived better when using habitat patches with high shrub cover and when using microhabitats with high protective cover. Numerous studies have reported that ungulate fawns bed down in dense ground cover (review in Mysterud and Ostbye 1999) but only a few studies have related habitat use to survival (e.g., Aanes and Andersen 1996; Canon and Bryant 1997; Farmer et al. 2006). In addition, studies on rodents (Moreno et al. 1996; Schooley et al. 1996; Ebensperger and Hurtado 2005) suggested that cover may be obstructive rather than protective for small mammals. Here we exploited a multivariate and hierarchical analysis of habitat use by juvenile porcupines to show that use of cover at both scales studied enhanced survival of one medium-bodied animal. This strong link between use of cover and survival was certainly due to the high predation risk on our study site. Other studies, performed in the absence of predators (and thus potentially in the absence of the selective pressures that shaped habitat selection), emphasized the importance of forage availability in the mothers' home range (Pettorelli et al. 2005; McLoughlin et al. 2007; Van Moorter et al. 2009) or thermal cover to enhance survival of juveniles (Van Moorter et al. 2009). Studies performed in presence of predators, on the other hand, emphasize the importance of cover as protection from predators (e.g., Aanes and Andersen 1996; Panzacchi et al. 2010; White et al. 2010). Use of cover therefore appears to have diverse ecological consequences, probably depending on the size of the study animal, and on the limiting factors with which it is faced (Mysterud and Ostbye 1999). Our 3rd prediction was supported because we found that most of the mortalities were due to predation and that use of cover enhanced survival. This confirmed that predation was more important than hypothermia in limiting survival of juveniles in our population, as supported by the evidence that habitat selection was driven by predator avoidance, even at fine scales of selection.

Sex, body mass on 10 June, mobility, distance to the mother, and survival.—Juveniles were not sexually dimorphic and we found no effect of sex or body mass on survival. Because predation was the main limiting factor in our population, we would expect increased body mass to enhance survival if larger (i.e., older) animals were less vulnerable to predators as in several other mammal species (white-tailed deer [*Odocoileus virginianus*—Nelson and Woolf 1987] and pronghorns [*Antilocapra americana*—Fairbanks 1993]). Even though males were not heavier than females, sex also could have influenced survival because of sex differences in behavior (Webb 1993). We observed juvenile porcupines to stay still when approached, whatever their size and sex. Males and heavier (older) juveniles did not show higher escape speed or aggressiveness compared to other juveniles (G. Mabille, pers. obs.). Therefore, it is not surprising they did not survive better.

We also found no effect of mobility on survival of juveniles. Juveniles are often argued to suffer high predation risk during dispersal because of greater activity rates, lower familiarity with new habitats, or use of lower-quality habitats (Gaines and McClenaghan 1980; Yoder et al. 2004). We expected more active individuals to show decreased survival because of higher exposure to predation risk. Juvenile porcupines mainly performed small movements (< 100 m) on a daily basis. However, porcupines were sometimes observed to move longer distances (up to 500 m) that could have exposed them to the same risks as dispersing animals. In "hider" species, mothers initiate the changes in location and accompany their young during long moves (Lent 1974). They also certainly influence the choice of the immigration area, even though the exact location of the new hiding site depends upon the juvenile (Lent 1974). One previous study (Stuart-Smith and Boutin 1995) investigated whether movements made by juvenile red squirrels (*Tamiasciurus hudsonicus*) before weaning (i.e., when they were still dependent on mother for food) influenced survival. This work found no effect of total movements on survival but found that individuals that spend relatively more time outside of their natal territory were more likely to be depredated. We suggest that the presence of the mother in the vicinity of the juvenile, and the fact that the mothers probably choose the stand where they would leave their young, largely reduced the risks usually associated with movements in dispersing juveniles.

Finally, we found no effect of the distance between juvenile and mother on survival of the juvenile. Females from several hiding species have been shown to reduce their home range during rearing of their young (Fisher and Goldizen 2001; Ciuti et al. 2006). This may allow females to feed their young more regularly and, in some species, to alert the young of an approaching danger (gazelles [*Eudorcas thomsonii*—Fitzgibbon 1993], and roe deer [*Capreolus capreolus*—Aanes and Andersen 1996]). We never observed mothers to warn their young or to protect them in any manner when we approached or captured juvenile porcupines. Still, females remained fairly close to their young, especially in their 1st weeks of life and we trust this could have enhanced juvenile survival if predation pressure had not been so high (Mabille et al. 2010).

Hiding juvenile mammals are (by definition) very difficult to find. This always constrains sample sizes and thus research designs. Few studies have thus tested hypotheses about the factors that shape habitat use and survival of hiding juvenile mammals, especially in a context where the predation pressures that may have shaped their hiding behavior are still present. Yet such research has potential relevance to our understanding of reproductive success, habitat use, predator–prey interactions, population dynamics, and evolutionary ecology of a large variety of species. Here, we used a rodent research model (the North American porcupine) never used before in such a context, to find clear effects of individual differences in juvenile habitat use on survival. Our study demonstrates the importance of comparing habitat use with measures of fitness to evaluate habitat suitability in neonates. It also clearly shows that hiding minimizes predation risk in species other than ungulates. We urge animal ecologists to continue expanding the taxonomical scope of such studies (ungulates constitute most research on the topic although they only represent 5% of mammal species—Wilson and Reeder 2005) to test the fitness implications of the hider–follower continuum of strategies with regard to predation risk.

Acknowledgments

We are grateful to C. Ndong M'ba, I. Klvana, P. Bergeron, E. Robert, K. Poitras, M.-C. Bedard, Y. Briand, G. Arguin, and J. Roberge for help in the field. We thank the personnel from Parc National du Bic for support during the project and S. Descamps and H. Wittmer for helpful comments on earlier drafts.

Literature Cited

Aanes, R., and R. Andersen. 1996. The effects of sex, time of birth, and habitat on the vulnerability of roe deer fawns to red fox predation. Canadian Journal of Zoology 74:1857–1865.

Alldredge, A. W., R. D. Deblinger, and J. Peterson. 1991. Birth and fawn bed site selection by pronghorns in a sagebrush-steppe community. Journal of Wildlife Management 55:222–227.

Allred, B. W., S. D. Fuhlendorf, T. J. Hovick, R. D. Elmore, D. M. Engle, and A. Joern. 2013. Conservation implications of native and introduced ungulates in a changing climate. Global Change Biology 19:1875–1883.

Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? Wildlife Monographs 134:1–50.

Bongi, P., et al. 2008. Anti-predator behaviour, space use and habitat selection in female roe deer during the fawning season in a wolf area. Journal of Zoology (London) 276:242–251.

Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? Journal of Mammalogy 79:415–425.

Campos, V. E., N. Andino, F. M. Cappa, M. L. Reus, and S. M. Giannoni. 2013. Microhabitat selection by *Octomys mimax* (Rodentia: Octodontidae) in the Monte Desert is affected by attributes and thermal properties of crevices. Revista Chilena de Historia Natural 86:315–324.

Canon, S. K., and F. C. Bryant. 1997. Bed-site characteristics of pronghorn fawns. Journal of Wildlife Management 61:1134–1141.

Cervinka, J., M. Salek, P. Pavluvcik, and J. Kreisinger. 2011. The fine-scale utilization of forest edges by mammalian mesopredators related to patch size and conservation issues in central European farmland. Biodiversity and Conservation 20:3459–3475.

Ciuti, S., P. Bongi, S. Vassale, and M. Apollonio. 2006. Influence of fawning on the spatial behaviour and habitat selection of female fallow deer (*Dama dama*) during late pregnancy and early lactation. Journal of Zoology (London) 268:97–107.

Compton, B. W., J. M. Rhymer, and M. McCollough. 2002. Habitat selection by wood turtles (*Clemmys insculpta*): an application of paired logistic regression. Ecology 83:833–843.

Comtois, A., and D. Berteaux. 2005. Impacts of mosquitoes and black flies on defensive behaviour and microhabitat use of the North American porcupine (*Erethizon dorsatum*) in southern Quebec. Canadian Journal of Zoology 83:754–764.

Côté, S. D., and M. Festa-Bianchet. 2001. Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. Oecologia 127:230–238.

Coulson, T., S. Albon, F. Guinness, J. Pemberton, and T. Clutton-Brock. 1997. Population substructure, local density, and calf winter survival in red deer (*Cervus elaphus*). Ecology 78:852–863.

Cox, D. R. 1972. Regression models and life-tables. Journal of the Royal Statistical Society, B. Statistical Methodology 34:187–220.

Demarchi, M. W., and F. L. Bunnell. 1993. Estimating forest canopy effects on summer thermal cover for Cervidae (deer family). Canadian Journal of Forest Research 23:2419–2426.

Dodge, W. E. 1982. Porcupine. Pp. 355–366 in Wild mammals of North America: biology, management, and economics (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins University Press, Baltimore, Maryland.

Dussault, C., J. P. Ouellet, R. Courtois, J. Huot, L. Breton, and J. Larochelle. 2004. Behavioural responses of moose to thermal conditions in the boreal forest. Ecoscience 11:321–328.

Ebensperger, L. A., and M. J. Hurtado. 2005. On the relationship between herbaceous cover and vigilance activity of degus (*Octodon degus*). Ethology 111:593–608.

Eberhardt, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

Fairbanks, W. S. 1993. Birth-date, birth-weight, and survival in pronghorn fawns. Journal of Mammalogy 74:129–135.

Farmer, C. J., D. K. Person, and R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. Journal of Wildlife Management 70:1403–1415.

Farrell, B. C., and D. P. Christian. 1987. Energy and water requirements of lactation in the North American porcupine, *Erethizon dorsatum*. Comparative Biochemistry and Physiology, A. Comparative Physiology 88:695–700.

Fisher, D. O., and A. W. Goldizen. 2001. Maternal care and infant behaviour of the bridled nailtail wallaby (*Onychogalea fraenata*). Journal of Zoology (London) 255:321–330.

Fitzgibbon, C. D. 1993. Antipredator strategies of female Thomson gazelles with hidden fawns. Journal of Mammalogy 74:758–762.

Fortin, D., H. L. Beyer, M. S. Boyce, D. W. Smith, T. Duchesne, and J. S. Mao. 2005. Wolves influence elk movements: behavior shapes a trophic cascade in Yellowstone National Park. Ecology 86:1320–1330.

Gaillard, J. M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J. M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toiego. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gaillard, J. M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84:3294–3306.

Gaines, M. S., and L. R. McClenaghan. 1980. Dispersal in small mammals. Annual Review of Ecology and Systematics 11:163–196.

Gilbert, B. A., and K. J. Raedeke. 2004. Recruitment dynamics of black-tailed deer in the western Cascades. Journal of Wildlife Management 68:120–128.

Gorini, L., et al. 2012. Habitat heterogeneity and mammalian predator–prey interactions. Mammal Review 42:55–77.

Grovenburg, T. W., R. W. Klaver, and J. A. Jenks. 2012. Survival of white-tailed deer fawns in the grasslands of the northern Great Plains. Journal of Wildlife Management 76:944–956.

Haim, A., R. J. van Aarde, and J. D. Skinner. 1992. Burrowing and huddling in newborn porcupine: the effect on thermoregulation. Physiology and Behavior 52:247–250.

Hoogland, J. L., K. E. Cannon, L. M. DeBarbieri, and T. G. Manno. 2006. Selective predation on Utah prairie dogs. American Naturalist 168:546–552.

Hosmer, D. W., and S. Lemeshow. 1989. Applied logistic regression. John Wiley & Sons, Inc., New York.

Huegel, C. N., R. B. Dahlgren, and H. L. Gladfelter. 1986. Bedsite selection by white-tailed deer fawns in Iowa. Journal of Wildlife Management 50:474–480.

Keech, M. A., R. T. Bowyer, J. M. Ver Hoef, R. D. Boertje, B. W. Dale, and T. R. Stephenson. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450–462.

Keller, F. L. 1935. Porcupines killed and eaten by a coyote. Journal of Mammalogy 16:232.

Kjellander, P., I. Svartholm, U. A. Bergvall, and A. Jarnemo. 2012. Habitat use, bed-site selection and mortality rate in neonate fallow deer *Dama dama*. Wildlife Biology 18:280–291.

Leclerc, M., C. Dussault, and M. H. St-Laurent. 2012. Multiscale assessment of the impacts of roads and cutovers on calving site selection in woodland caribou. Forest Ecology and Management 286:59–65.

Lent, P. C. 1974. Mother–infant relationships in ungulates. Pp. 14–54 in The behaviour of ungulates and its relation to management (V. Geist and F. Walther, eds.). International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.

Lin, D. Y., and L. J. Wei. 1989. The robust inference for the Cox proportional hazards model. Journal of the American Statistical Association 84:1074–1078.

Lingle, S., A. Feldman, M. S. Boyce, and W. F. Wilson. 2008. Prey behavior, age-dependent vulnerability, and predation rates. American Naturalist 172:712–725.

Linnell, J. D. C., R. Aanes, and R. Andersen. 1995. Who killed Bambi? The role of predation in the neonatal mortality of temperate ungulates. Wildlife Biology 1:209–223.

Mabille, G., D. Berteaux, D. W. Thomas, and D. Fortin. 2011. Behavioural responses of wintering porcupines to their heterogeneous thermal environment. Ecoscience 18:341–353.

Mabille, G., S. Descamps, and D. Berteaux. 2010. Predation as a probable mechanism relating winter weather to population dynamics in a North American porcupine population. Population Ecology 52:537–546.

Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. 2nd ed. Kluwer Academic Publishers, Norwell, Massachusetts.

Mathisen, J. H., A. Landa, R. Andersen, and J. L. Fox. 2003. Sex-specific differences in reindeer calf behavior and predation vulnerability. Behavioral Ecology 14:10–15.

May, R., J. van Dijk, J. M. Forland, R. Andersen, and A. Landa. 2008. Behavioural patterns in ewe–lamb pairs and vulnerability to predation by wolverines. Applied Animal Behaviour Science 112:58–67.

McLoughlin, P. D., et al. 2007. Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88:3192–3201.

Molinari-Jobin, A., P. Molinari, A. Loison, J. M. Gaillard, and U. Breitenmoser. 2004. Life cycle period and activity of prey influence their susceptibility to predators. Ecography 27:323–329.

Moreno, S., R. Villafuerte, and M. Delibes. 1996. Cover is safe during the day but dangerous at night: the use of vegetation by European wild rabbits. Canadian Journal of Zoology 74:1656–1660.

Morin, P., and D. Berteaux. 2003. Immobilization of North American porcupines (*Erethizon dorsatum*) using ketamine and xylazine. Journal of Wildlife Diseases 39:675–682.

Morin, P., D. Berteaux, and I. Klvana. 2005. Hierarchical habitat selection by North American porcupines in southern boreal forest. Canadian Journal of Zoology 83:1333–1342.

Mysterud, A., and E. Ostbye. 1999. Cover as a habitat element for temperate ungulates: effects on habitat selection and demography. Wildlife Society Bulletin 27:385–394.

Nelson, T. A., and A. Woolf. 1987. Mortality of white-tailed deer fawns in southern Illinois. Journal of Wildlife Management 51:326–329.

Nielson, S. E., M. S. Boyce, G. B. Stenhouse, and R. H. M. Munro. 2002. Modeling grizzly bear habitats in the Yellowhead ecosystem of Alberta: taking autocorrelation seriously. Ursus 13:45–56.

Norrdahl, K., and E. Korpimaki. 1998. Does mobility or sex of voles affect risk of predation by mammalian predators? Ecology 79:226–232.

Olson, K. A., T. K. Fuller, G. B. Schaller, B. Lhagvasuren, and D. Odonkhuu. 2005. Reproduction, neonatal weights, and first-year survival of Mongolian gazelles (*Procapra gutturosa*). Journal of Zoology (London) 265:227–233.

Panzacchi, M., I. Herfindal, J. D. C. Linnell, M. Odden, J. Odden, and R. Andersen. 2010. Trade-offs between maternal foraging and fawn predation risk in an income breeder. Behavioral Ecology and Sociobiology 64:1267–1278.

Pettorelli, N., et al. 2005. The response of fawn survival to changes in habitat quality varies according to cohort quality and spatial scale. Journal of Animal Ecology 74:972–981.

Piccolo, B. P., T. R. Van Deelen, K. Hollis-Etter, D. R. Etter, R. E. Warner, and C. Anchor. 2010. Behavior and survival of white-tailed deer neonates in two suburban forest preserves. Canadian Journal of Zoology 88:487–495.

Powell, R. A., and R. B. Brander. 1977. Adaptations of fishers and porcupines to their predator prey system. Pp. 45–53 in Proceedings for 1975 predator symposium (R. L. Phillips and C. Jonkel, eds.). Montana Forest Conservation Experimental Station, University of Montana, Missoula.

Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. Journal of Zoology (London) 245:457–465.

Rearden, S. N., R. G. Anthony, and B. K. Johnson. 2011. Birth-site selection and predation risk of Rocky Mountain elk. Journal of Mammalogy 92:1118–1126.

Rettie, W. J., and F. Messier. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

Robinette, W. L., J. S. Gashwiler, and O. W. Morris. 1959. Food habits of the cougar in Utah and Nevada. Journal of Wildlife Management 23:261–273.

Roze, U. 2009. The North American porcupine. 2nd ed. Cornell University Press, Ithaca, New York.

Salek, M., J. Kreisinger, F. Sedlacek, and T. Albrecht. 2010. Do prey densities determine preferences of mammalian predators for habitat edges in an agricultural landscape? Landscape and Urban Planning 98:86–91.

SAS Institute Inc. 2004. SAS statistical software. Version 9.1.3. SAS Institute Inc., Cary, North Carolina.

Scheffers, B. R., D. P. Edwards, A. Diesmos, S. E. Williams, and T. A. Evans. 2014. Microhabitats reduce animal's exposure to climate extremes. Global Change Biology 20:495–503.

Schooley, R. L., P. B. Sharpe, and B. VanHorne. 1996. Can shrub cover increase predation risk for a desert rodent? Canadian Journal of Zoology 74:157–163.

Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 92:235–253.

Stuart-Smith, A. K., and S. Boutin. 1995. Behavioural differences between surviving and depredated juvenile red squirrels. Ecoscience 2:34–40.

Sweitzer, R. A., and J. Berger. 1992. Size-related effects of predation on habitat use and behavior of porcupines (*Erethizon dorsatum*). Ecology 73:867–875.

van Beest, F. M., B. Van Moorter, and J. M. Milner. 2012. Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. Animal Behaviour 84:723–735.

Van Moorter, B., J. M. Gaillard, P. D. McLoughlin, D. Delorme, F. Klein, and M. S. Boyce. 2009. Maternal and individual effects in selection of bed sites and their consequences for fawn survival at different spatial scales. Oecologia 159:669–678.

Webb, N. J. 1993. Growth and mortality in juvenile European wild rabbits (*Oryctolagus cuniculus*). Journal of Zoology (London) 230:665–677.

Wei, L. J., D. Y. Lin, and L. Weissfeld. 1989. Regression-analysis of multivariate incomplete failure time data by modeling marginal distributions. Journal of the American Statistical Association 84:1065–1073.

White, C. G., P. Zager, and M. W. Gratson. 2010. Influence of predator harvest, biological factors, and landscape on elk calf survival in Idaho. Journal of Wildlife Management 74:355–369.

Wilson, D. E., and D. M. Reeder (eds.). 2005. Mammal species of the world: a taxonomic and geographic reference. 3rd ed. Johns Hopkins University Press, Baltimore, Maryland.

Yoder, J. M., E. A. Marschall, and D. A. Swanson. 2004. The cost of dispersal: predation as a function of movement and site familiarity in ruffed grouse. Behavioral Ecology 15:469–476.

Submitted 27 November 2013. Accepted 28 April 2014.

Associate Editor was Harald Beck.