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ORIGINAL ARTICLE

Predation as a probable mechanism relating winter weather to population dynamics in a North American porcupine population

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Abstract An abundance index of an eastern Quebec population of North American porcupines (*Erethizon dorsatum*) has cycled with superimposed periodicities of 11 and 22 years from 1868 to 2000. This cycle closely followed 11- and 22-year cycles in solar irradiance and local weather (e.g., winter precipitation and spring temperature), generating the hypothesis that solar activity may affect porcupine abundance through effects on local weather. We investigated the mechanisms linking porcupine abundance to local weather conditions using a 6-year study (2000–2005) involving individual mark-recapture, radio tracking, seasonal survival analyses and identification of mortality causes. Summer (May–August) survival was high and constant over the study period, whereas winter (August–May) survival was lower and varied during the duration of our study. Variations in local winter precipitation explained 89% of the variation in winter survival. Porcupine predation rates appeared strongly related to snow conditions; 95% of depredated porcupines were killed when snow was covering the ground, and predation rates were higher in years with increased winter precipitation. Our data thus support the hypothesis that changes in predation rates under different snow conditions were the mechanism relating climate to porcupine population dynamics, via modifications of the local predator–prey interactions and impacts on porcupine winter survival. Our study adds to the growing body of evidence supporting an effect of climate on predator–prey processes. Also, it identifies one possible mechanism involved in the relationship between solar irradiance and porcupine population cycles observed at this study site over a 130-year period.

Keywords Climate · Fisher · Predator–prey · Seasonal survival · Solar cycle · Species interaction

Introduction

Climate is often a major determinant of animal population dynamics (Saether et al. 2004; Krebs and Berteaux 2006). Climate can have direct effects on individuals with, for example, winter weather affecting locomotion (Telfer and Kelsall 1984) or thermoregulation (Cook et al. 1998). However, climate can also have indirect effects by influencing species interactions. For example, deep snow may influence predator–prey relationships (Post et al. 1999; Hebblewhite 2005) and access to food resources (Post and Stenseth 1999). How climate influences population dynamics is complex, and our understanding of mechanisms linking climate to population growth is limited.

Large-scale climate manipulations are not feasible, and testing for specific changes driven by weather variations is plagued by experimental difficulties. Therefore, the two main approaches that have been used to investigate the effects of climate are: (1) small-scale studies investigating mechanisms linking weather to population biology, and (2) large-scale studies, over long time periods or large areas, correlating climatic variability with changes in population parameters. Both approaches have advantages and drawbacks (Berteaux et al. 2006), and Root and Schneider

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(1995) suggested alternating large- and small-scale studies to further climate research. In such cycles of analysis, large-scale studies generate models and hypotheses to feed small-scale mechanistic studies, while small-scale studies test hypotheses and allow refinement of large-scale models.

The solar cycle may have an impact on weather (e.g., Tsiropoula 2003) with cascading effects on entire ecosystems (Sinclair et al. 1993; Klvana et al. 2004). For instance, the reproductive output of snowshoe hares (*Lepus americanus*) in Yukon was cyclic and highly correlated with sunspot numbers with a 2-year time lag (Stefan and Krebs 2001; Krebs and Berteaux 2006). Possible mechanisms include an effect of solar activity on snow depth, which might in turn affect hare food supplies (Krebs and Berteaux 2006) and lynx hunting success (Stenseth et al. 1999, 2004). North American porcupine (*Erethizon dorsatum*) populations in eastern Quebec may also be affected by the solar cycle (Klvana et al. 2004). Porcupines are medium-sized herbivorous mammals that do not hibernate, and are preyed upon by a variety of mammalian and avian predators (Roze 2009). Klvana et al. (2004) found that the annual frequency of porcupine feeding scars (an index of porcupine abundance) in eastern Quebec cycled with the same periodicities (11 and 22 years) as solar activity, local winter precipitation, and local spring temperature. The phase dependence between the above variables was remarkably constant over a 130-year period, generating the hypotheses that solar activity could influence local weather which, in turn, may influence porcupine population dynamics. As suggested for hares (Krebs and Berteaux 2006), solar activity and porcupine abundance could be linked through snow conditions, which may affect food access (Roze 2009) or predator exposure (Thibault and Ouellet 2005). The solar activity could also influence spring temperature which, in mammals, can have direct effects on thermoregulation of juveniles (Haim et al. 1992) or indirect effects on individual condition by impacting vegetation growth (Langvatn et al. 1996; Post and Stenseth 1999). Following the approach suggested by Root and Schneider (1995), we used hypotheses generated by Klvana et al. (2004) to design a study aimed at better understanding the causal relationships between local weather (e.g., winter precipitation and spring temperature), and porcupine abundance.

From 2000 to 2005, we conducted a mark–recapture study on a population of porcupines in eastern Quebec. Intensive fieldwork in May and August facilitated estimates of annual population size, as well as annual “summer” (May–August) and “winter” (August–May) survival rates, to be determined. In addition, we used radio-telemetry throughout the year to locate dead porcupines and identify mortality causes. We first tested for correlations between local weather and porcupine abundance. Then, because North American porcupines are long-lived (up to 18 years; Roze 2009), and adult survival has the largest influence on changes in abundance in long-lived vertebrates (Gaillard et al. 2000; Eberhardt 2002), we investigated the relationship between local weather and survival of porcupines. We predicted that an increase in winter precipitation and a decrease in spring temperature should be associated with a decline in porcupine survival.

Finally, we tested some mechanistic hypotheses linking weather conditions to porcupine survival. We selected four non-exclusive mechanisms based on a priori knowledge which led to four specific predictions:

1. Effects of spring temperature on starvation and summer survival of juveniles; young mammals are sensitive to hypothermia because of their immature thermoregulatory system (Hull 1973). We predicted that low spring temperature should increase the probability of starvation in juveniles with immature thermoregulatory systems and, due to lagged effects on body condition, decrease their summer (May–August) survival.
2. Effects of spring temperature on starvation and winter survival; low spring temperature can decrease primary productivity (Langvatn et al. 1996), which can in turn reduce herbivores’ fall body condition and winter survival (Loison and Langvatn 1998). We predicted that low spring temperature should decrease winter (August–May) survival of porcupines, through an increase in the probability of starvation.
3. Effects of winter precipitation on starvation and winter survival; snow cover impedes movements of porcupines and decreases their access to food (Roze 1984). We predicted that high winter precipitation should decrease winter survival of porcupines due to mobility constraints in snow and increase the likelihood of starvation.
4. Effects of winter precipitation on predation and winter survival; snow can affect predatory behaviour (e.g., Lindstrom and Hornfeldt 1994; Jedrzejewski et al. 2002), and prey living above the snow surface usually suffer higher predation risk as snow deepens (Post et al. 1999; Hebblewhite 2005). We predicted that high winter precipitation, which impedes porcupine movement, should increase porcupine depredation rates and decrease their winter survival.

Materials and methods

Study population and field methods

Work was conducted from May 2000 to 2005 in an area approximately 2 km^2 of Parc National du Bic (48°20′N, 68°46′W, elevation 0–150 m), Quebec, Canada. The study area includes previously and currently cultivated fields, and mixed boreal forest (see S1 in Electronic Supplementary Material, ESM). The topography is rugged with an abundance of natural rock dens. We captured porcupines in open fields during intensive capture sessions in May and August 2000–2004 and May 2005 (see S2 in ESM). Each survey night involved one to six observers (typically two) who patrolled the study area on foot or bicycle for 1–9 h (typically 5). We sexed, weighed, aged (as juvenile, subadult, or adult using body mass in May; see Berteaux et al. 2005 for details), and permanently marked porcupines upon capture with colored plastic and metal ear tags (Berteaux et al. 2005; Morin et al. 2005). We used recaptures, visual observations, and radio collars (Lotek SMRC-5RB VHF transmitters; Lotek Wireless, Newmarket, Canada; $n = 97$ individuals for 23,576 porcupine-days; see S2 in ESM) to monitor the fate of individuals (survival vs. mortality).

The parturition period is mid-May to late June so we considered a population-year to start on 1 May (e.g., year 2000 extends from 1 May 2000 to 30 April 2001). We estimated the minimum population size for a given year as the number of different individuals observed alive at least once between 1 May of that year and 30 April of the following year. Adult porcupines feed in open fields during summer (especially in May when tree leaves are not yet available), which facilitated their detection by observers. We are confident that virtually all adult porcupines present in the study area were captured or resighted at least once a year. This was confirmed by winter den observations that rarely yielded unmarked adult individuals. Overall, only seven individuals (three in 2001 and four in 2002, representing 4 and 6% of the total number of captured porcupines, respectively) were not observed in a given year but found to be alive in a subsequent year (these individuals were included in estimates of population size for the year in which they had not been observed).

Relationships between local weather variables and changes in porcupine abundance

We used estimates of population size to calculate population growth rate as:

$$\lambda_t = N_{t+1}/N_t \tag{1}$$

in which λ_t is population growth rate for year t, N_t is population size in year t and N_{t+1} is population size in the following year. We used Pearson correlations to test for statistical associations between population growth rate and local weather variables. Based on Klvana et al. (2004), we considered three weather variables: winter precipitation (total precipitation in mm, from 1 November to 30 April), snowfall (in cm, same time period) and spring temperature (mean monthly temperature in °C, averaged over May and June). We obtained weather records from the Rimouski Environment Canada weather station (48°27′N, 68°31′W), located approximately 20 km from our study site. We standardized [(value − mean)/SD] weather data prior to analyses.

Seasonal survival rates

Survival analyses did not include porcupines that died from research related causes. Our dataset consisted of 82 females (12 captured initially as juveniles, 16 as subadults, and 54 as adults) and 77 males (16 captured initially as juveniles, 7 as subadults, and 54 as adults). Preliminary analyses indicated that survival was similar for subadults and adults, so we only considered two age classes, juveniles and individuals $\geq$1 year old. We used methods detailed in Loison et al. (1994) to include different ages at capture in the estimation procedures. We estimated seasonal survival rates of porcupines from May 2000 to May 2005 ($k = 11$ occasions of captures). We defined survival from May to August and from August to May as "summer" and "winter" survival, respectively. The lengths of our summer and winter periods were thus 4 and 8 months, respectively. We performed survival analyses using capture–mark–recapture (CMR) methods (Lebreton et al. 1992), with the program M-SURGE 1.7.1 (Choquet et al. 2004) which can take into account unequal interval lengths between capture occasions.

The fit of our data to the Cormack–Jolly–Seber (CJS) model was acceptable (goodness-of-fit test using U-CARE 2.2.5; Choquet et al. 2003: $\chi^2 = 32.0$, $df = 23$, $P = 0.1$), even though all animals were not equally likely to be resighted at least once ($\chi^2 = 31.0$, $df = 9$, $P < 0.001$, component 3.Sr of the goodness-of-fit test). This heterogeneity in resighting probabilities was caused by the use of telemetry on some porcupines. Multi-state CMR modelling (with two states: individual fitted with a radio collar at time t, or individuals not fitted with a radio collar at time t), taking into account this heterogeneity in resighting probabilities, led to similar results as simple CMR modelling; results from the latter approach are presented. We carried out model selection using the Akaike Information Criterion corrected for small sample sizes (AICc; Burnham and Anderson 2002). We considered models that were within two units of AICc (ΔAICc < 2) to be equally competitive to explain the data (Burnham and Anderson 2002), and retained the simplest one when two nested models were within two units of AICc.

Since survival rates are the parameters of interest in our study, we first modeled resighting rates (see S3 in ESM) to have increased statistical power when modeling survival (Lebreton et al. 1992). We tested for the effects of sex and age on survival, as North American porcupines are sexually dimorphic (Roze 2009), and mammalian populations are commonly age-structured (Charlesworth 1994). Following the hypotheses generated by Klvana et al. (2004), we then tested for effects of winter precipitation, snowfall, and spring temperature on survival rates. Because time-lag effects of weather on phenotypic and demographic traits can be important (Post and Stenseth 1999), we tested for direct and delayed (lags 1–2 years) effects of weather on survival. We used standardized weather data for analyses.

The proportion of yearly variations in survival that is explained by a given weather covariate was calculated as follows (Schemper 1990):

$$r^2 = \frac{\text{Deviance (covariate)} - \text{Deviance (constant)}}{\text{Deviance (year)} - \text{Deviance (constant)}} \quad (2)$$

where covariate, year and constant refer to the models with covariate-dependent, time-dependent, and constant survival rates.

Causes of mortality

We located dead porcupines during surveys or by radio-telemetry ($n = 13$ and 47 dead individuals, respectively). We did not perform telemetry during winter 2001 and during 2005 (see S2 in ESM), thus we considered that searching effort was insufficient in those periods ($n = 4$ carcasses found) and excluded them from analyses. Three porcupines died during anaesthesia and three mortalities were attributed to collars becoming entangled in trees. We excluded these six individuals from analyses, and therefore examined causes of mortality for 50 animals that died in 2000, 2002, 2003, and 2004. We classified cause of death into five categories (1) dead from starvation (not injured but emaciated), (2) road kills, (3) dead from tree fall (injured and found under a tree), (4) predator killed, or (5) unknown. We considered a porcupine as killed by a predator when its radio collar was retrieved and bore visible traces of blood ($n = 8$), or when we found remains of skin, intestines, or stomach (Sweitzer 1996) on carcasses ($n = 20$). Sweitzer (1996) specifically used the presence of intestines or stomach on carcasses to discriminate depredated porcupines from scavenged carcasses. In addition, we examined most carcasses shortly (i.e., 1–2 days) after we determined mortality from the audible change in the telemetry signal. We are therefore confident that porcupines we considered killed by predators were actually depredated animals and did not die from other causes and were later scavenged. Potential predators in our study site included fishers (*Martes pennanti*), coyotes (*Canis latrans*), and great horned owls (*Bubo virginianus*). We recorded the identity of the predator species when possible (e.g., by identifying snow tracks around depredated porcupines).

We used G tests (Sokal and Rohlf 1981) to compare the causes of mortality across years, and between age classes (two age classes: juveniles and individuals ≥ 1 year old). Predation and starvation were the two main causes of mortality in our population, so we also used G tests to evaluate whether proportions of juveniles and individuals ≥ 1 year old dying from predation and starvation were different between seasons (summer vs. winter). Because we hypothesized that the presence of snow cover could affect predation and starvation rates, we further divided the winter season into two periods when analyzing causes of mortality: "winter/no snow" (1 September to first snow fall date, generally mid-November), and "winter/snow" (first snow fall date, generally mid-November to 30 April). Results are presented as mean ± SE.

Results

Relationships between local weather variables and changes in porcupine abundance

We observed a strong decline in porcupine abundance of all age classes in our study population, from 117 individuals in 2000 to only 4 individuals in 2005 (Table 1). Consistently, annual population growth rate was <1 and varied from 0.72 in 2000 to 0.17 in 2004 (Table 1). Annual population growth rate was negatively correlated with winter precipitation ($r = -0.97$, $P = 0.006$, $n = 5$) and snowfall ($r = -0.84$, $P = 0.07$, $n = 5$), but the latter correlation was not significant at the 5% level. Population growth rate was not correlated to spring temperature ($r = 0.56$, $P = 0.3$, $n = 5$) (Fig. 1).

Table 1 Age structure and minimum population size of North American porcupines (*Erethizon dorsatum*) studied in Parc National du Bic, Quebec, Canada, May 2000–May 2005

	2000	2001	2002	2003	2004	2005
Juvenile males[a]	7	1	4	3	2	0
Juvenile females[a]	2	3	1	3	3	0
Subadult males	6	2	2	0	0	0
Subadult females	10	3	2	0	2	0
Adult males	47	38	27	17	7	1
Adult females	45	37	30	21	9	3
Total	117	84	66	44	23	4
Growth rate	0.72	0.79	0.67	0.52	0.17	

Population growth rate in year t was calculated as population size in year $t + 1$ divided by population size in year t

[a] We searched for juveniles around lactating females and search effort was insufficient to find all juveniles present in the study area. Numbers presented here therefore do not reflect the actual number of juveniles present in the population

Seasonal survival rates

Survival of porcupines varied with age and season (Table 2); juveniles exhibited lower survival than individuals $\geq$1 year old, regardless of season. As shown in Fig. 2, summer survival was high and constant over the study period (mean monthly summer survival ± SE: 0.85 ± 0.04 for juveniles and 0.97 ± 0.01 for individuals $\geq$1 year old) while winter survival was lower and variable from year to year (mean monthly winter survival: 0.53–0.82 for juveniles and 0.85–0.96 for individuals $\geq$1 year old). Winter precipitation explained 89% of the yearly variations in winter survival (Table 3), with winter survival being negatively related to winter precipitation (Fig. 2). The model including winter precipitation was preferred over the model including a year effect (ΔAICc = 5.699; Table 3). Snowfall alone explained a moderate amount of variation in winter survival (53%), whereas spring temperature explained little variation (9%; Table 3). We found no evidence of a lag effect of winter precipitation, snowfall, or spring temperature (1 or 2 years) on winter survival (see S4 in ESM).

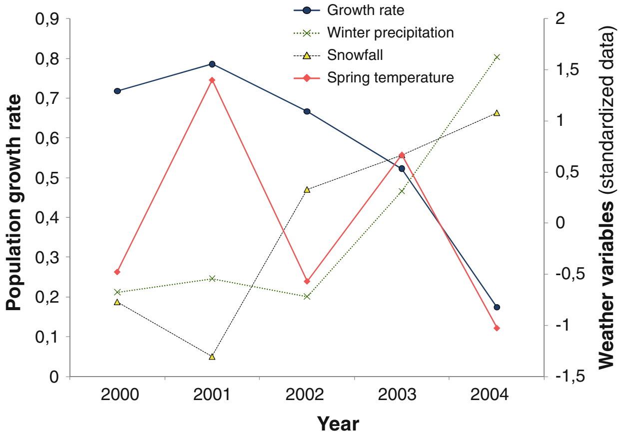

Fig. 1 Population growth rate (*left* axis, population size in year *t*/population size in year $t + 1$) as observed in a North American porcupine (*Erethizon dorsatum*) population followed by capture–mark–recapture in Parc National du Bic, QC, Canada, May 2000–2005. The *right* axis shows standardized weather variables used to test for correlations with population growth rate: winter precipitation (November, year *t* to April, year $t + 1$), snowfall (November, year *t* to April, year $t + 1$), and spring temperature (May–June, year *t*). Weather records were obtained from the Rimouski Environment Canada weather station (48°27′N, 68°31′W), located about 20 km from our study site

Causes of mortality

We could confidently assign a cause of mortality to 46 of 50 porcupines examined. Predation ($n = 28$, 60.9%) and starvation ($n = 13$, 28.3%) were the primary causes of mortality. Fall from a tree ($n = 3$) and road kill ($n = 2$) together represented 10.8% of mortalities. We determined identities of the predator species for 14 of the 28 predation events; fishers were responsible for 86% ($n = 12$) and coyotes for 14% ($n = 2$). The proportion of mortalities due to predation vs. other known causes (i.e., starvation, tree fall, and road kill combined) was not constant through time ($G = 8.640$, $df = 3$, $P = 0.034$) and increased from 40% in 2000 and 2002 to 91.7% in 2004 (Fig. 3). Mortality due to predation was so high in 2004 that we did not observe any starvation or road kill in this year (Fig. 3). The proportion of mortalities due to predation was strongly positively correlated to the amount of winter precipitation ($r = 0.99$, $P = 0.005$, $n = 4$).

Causes of mortality did not differ between age classes ($G = 1.399$, $df = 3$, $P = 0.7$; see S5 in ESM). Among depredated animals (6 juveniles, and 22 $\geq$ 1 year old), timing of death differed between age classes ($G = 26.324$, $df = 2$, $P < 0.001$). Juveniles were depredated primarily in summer (83.3% in summer vs. 16.7% in winter; Fig. 4a)

Table 2 Model selection for seasonal survival rates (ϕ) in a population of North American porcupines, Parc National du Bic, QC, Canada, May 2000–2005

Biological meaning	Notation	Deviance	np	ΔAICc[a]
Year effect in winter only, and age effect	$\boldsymbol{\phi_a^{\mathrm{U}}\ \phi_{y+a}^{\mathrm{W}}}$	**789.984**	**13**	**0.000**
Additive effect of year, season and age	ϕ_{y+s+a}	794.042	13	4.058
Additive effect of time and age	ϕ_{t+a}	786.196	17	6.042
Additive effect of year and age	ϕ_{y+a}	798.752	12	6.395
Year effect in summer only, and age effect	$\phi_{y+a}^{\mathrm{U}}\ \phi_a^{\mathrm{W}}$	799.584	13	9.600
Additive effect of time and sex	$\phi_{t+\mathrm{sex}}$	811.139	17	30.985
Constant survival	ϕ	835.205	7	31.453

We used data on 159 individuals. We modeled resighting probabilities following model selected in Table 2. We tested for the effects of sex, age (*a*, considering two age classes: juveniles and $\geq$1-year old), season (*s*) and year (*y*). The most parsimonious model is in bold

U Summer, *W* winter, *np* number of estimated parameters, Δ*AICc* difference in AICc from the selected model

[a] Effect of time *t* is equivalent to a *y.s* effect

and individuals ≥1 year old exclusively in winter, and almost exclusively when snow cover was present (95.5% when snow cover present; Fig. 4a). Among starved animals (2 juveniles, 11 individuals ≥1 year old), timing of death did not differ between age classes ($G = 0.731$, $df = 2$, $P = 0.7$) with most of the starvations (juveniles: 100%; individuals ≥1 year old: 81.8%; Fig. 4b) occurring when snow was covering the ground.

Discussion

Relationships between local weather variables and changes in porcupine abundance

We observed a strong decline in porcupine abundance from 2000 onwards. This was not due to our repeated captures increasing disturbance or emigration of porcupines, since similar results emerged from surveys of porcupine den occupancy in areas of Parc National du Bic where we did not perform captures (Y. Lemay, unpublished data). Short-term changes in abundance of porcupines derived from CMR data were correlated with winter precipitation and snowfall. This finding confirms the long-term correlations between local weather and porcupine abundance found by Klvana et al. (2004) using indirect evidence of porcupine abundance (i.e., feeding scars on trees left by porcupines). However, our study did not support the association between porcupine abundance and spring temperature described by Klvana et al. (2004). We further discuss our results in the context of the possible relationships between local weather and fluctuations in porcupine abundance.

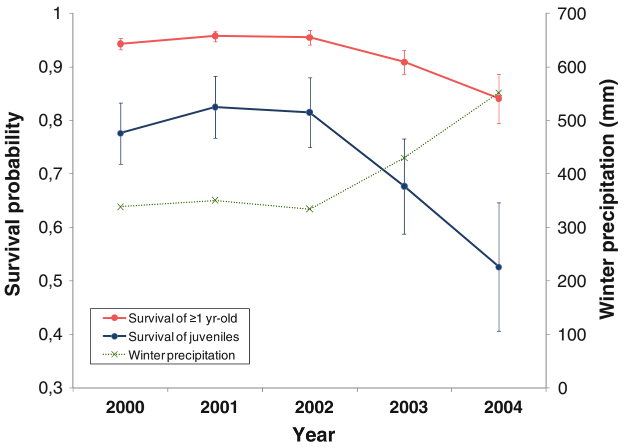

Fig. 2 Mean monthly survival probability (*left* axis) between August in year t and May in year $t + 1$ according to age (juveniles and individuals ≥1 year old) in a North American porcupine population, Parc National du Bic, QC, Canada, August 2000–May 2005. Results correspond to point estimates (mean ± SE) from the model selected in Table 2. The *right* axis shows the environmental covariate most related to winter survival: winter precipitation (in mm, measured from November, year t to April, year $t + 1$)

Seasonal survival rates

Survival has the largest demographic influence on changes in abundance of long-lived vertebrates, and we expected survival rates of porcupines to be influenced by local weather. Our study site is located in a highly seasonal temperate environment, exposing animals to contrasting weather conditions that may affect survival in different ways. Seasonal survival rates are crucial to understanding how mortality risks faced by animals vary during their annual cycle, or with changing weather conditions. Reliable estimates of seasonal survival rates are infrequent in mammals (e.g., Crespin et al. 2002; Lima et al. 2002), and factors affecting survival on a seasonal basis have been poorly explored (Gauthier et al. 2001). Calculating seasonal survival rates of porcupines allowed us to establish that summer survival was constant, and to identify winter as the most critical phase of the annual cycle for porcupine survival during our study period. This was not surprising as winter is often a decisive period for herbivorous mammals, due to high energy demand and availability of low quality forage (Halfpenny and Ozanne 1989). However, we also found that winter precipitation explained a large percentage (89%) of

Table 3 Tests of the effects of local weather variables on winter survival rates (ϕ^{W}) in a population of North American porcupines, Parc National du Bic, QC, Canada, May 2000–2005

Biological meaning	Notation	Deviance	np	ΔAICc	r^2
Winter survival dependent on winter precipitation, and age effect	$\boldsymbol{\phi_a^{\mathrm{U}}\ \phi^{\mathrm{W}}_{\mathrm{Precipitations}+a}}$	**791.309**	**10**	**0.000**	**0.89**
Winter survival dependent on snowfall, and age effect	$\phi_a^{\mathrm{U}}\ \phi^{\mathrm{W}}_{\mathrm{Snowfall}+a}$	795.883	10	4.574	0.53
Winter survival dependent on year, and age effect, from Table 3	$\phi_a^{\mathrm{U}}\ \phi^{\mathrm{W}}_{y+a}$	789.984	13	5.699	1
No yearly variation in winter survival, and age effect	$\phi_a^{\mathrm{U}}\ \phi^{\mathrm{W}}_{a}$	802.486	9	8.899	0
Winter survival dependent on spring temperature, and age effect	$\phi_a^{\mathrm{U}}\ \phi^{\mathrm{W}}_{\mathrm{Spring}+a}$	801.331	10	10.022	0.09

We used data on 159 individuals. The most parsimonious model is bolded. We show the proportion of yearly variation in survival (r^2) that is explained by each weather covariate

U Summer, *W* winter, *y* year, *a* age modeled as two age classes (juveniles, ≥1 year old), *np* number of estimated parameters, Δ*AICc* difference in AICc from the selected model

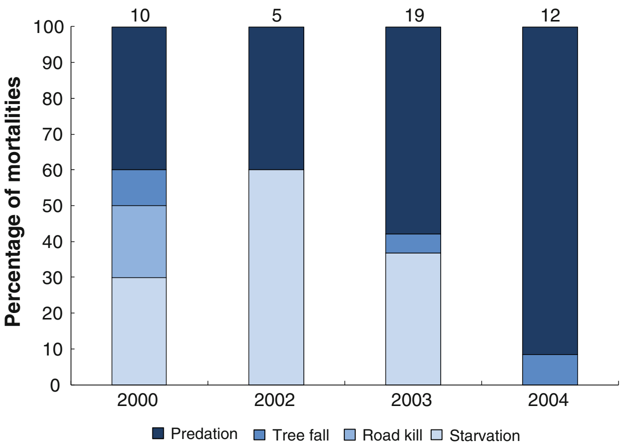

Fig. 3 Known causes of mortality as observed in North American porcupines found dead in Parc National du Bic, QC, Canada, May 2000–April 2005. Annual sample sizes are indicated above *bars*

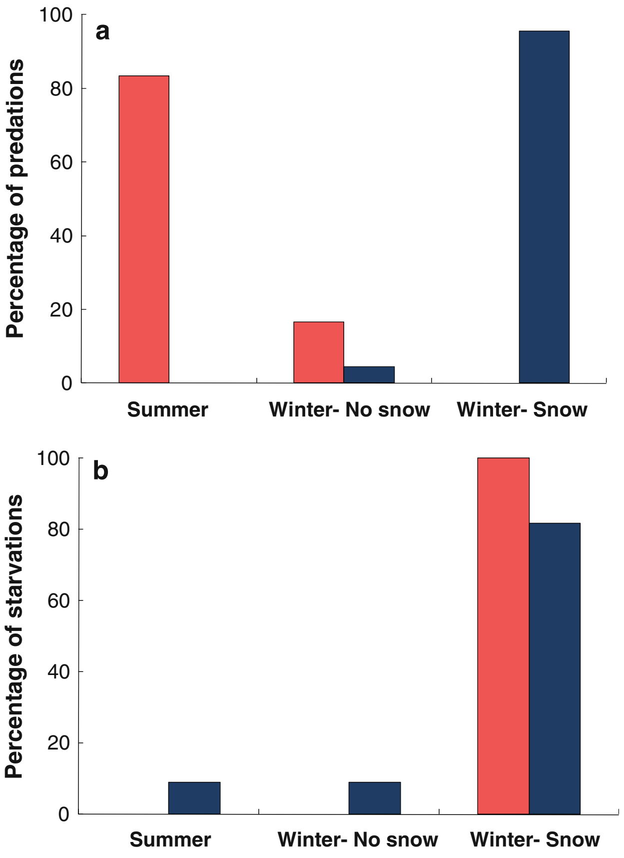

Fig. 4 Seasonal timing of death for North American porcupines, Parc National du Bic, Quebec, Canada, May 2000–April 2005. **a** Juveniles ($n = 6$, *light bars*) and individuals ≥ 1 year old ($n = 22$, *dark bars*) killed by predators; **b** juveniles ($n = 2$, *light bars*) and individuals ≥ 1 year old ($n = 11$, *dark bars*) that died from starvation. Seasons were defined as: summer (1 May to 31 August), winter/no snow (1 September to first snow fall, generally mid-November), and winter/snow (first snow fall, generally mid-November to 30 April)

the variability observed in winter survival, with low levels of winter precipitation being associated with high winter survival. Studies investigating how weather variables affect demographic parameters of homeotherms typically explain at most 50–90% of observed variation (Post and Stenseth 1999; Owen-Smith et al. 2005; Sandvik et al. 2008). In our study, winter survival therefore appeared to be closely related to changes in weather conditions that could in turn influence starvation or predation rates.

Mechanisms linking winter precipitation to winter survival

Based on a priori knowledge of the ecology of North American porcupines, we formulated two non-exclusive hypotheses to explain the effect of winter precipitation on winter survival rates of porcupines (see "Introduction", predictions 3 and 4). One hypothesis was based on an increased probability of porcupine starvation due to mobility constraints (Roze 1984) and hindered access to food resources, and the other on an increase of predation rates on porcupines because of changes in predator behavior. Our examination of the causes of mortality indicated that predation was the primary mortality factor in our population, and that predation rates were higher in years of high winter precipitation (e.g., 2004). In fact, predation rates were so high in 2004 that we did not observe any death by starvation that year, whereas starvation represented a significant mortality factor in the previous years (30–60% of all mortalities in 2000, 2002, and 2003). Also, predators killed adult porcupines almost exclusively when snow was covering the ground. North American porcupines are short-limbed animals and presence of snow cover may increase predation risk for porcupines, either directly by reducing their ability to escape (Huggard 1993) or indirectly because starving animals may be more susceptible to predators (Sweitzer 1996). Furthermore, predators may shift to more vulnerable prey (Patterson et al. 1998), such as porcupines, when snow is more abundant. Fishers, the main predators of porcupines in our study area, are very efficient at killing porcupines (Powell 1993), and their numbers have rapidly increased in eastern Quebec since the mid-1990s (Poulin et al. 2006). They feed primarily on snowshoe hares (Powell 1993), but may switch to porcupines when snow depth increases. Snowshoe hares have a low foot-load (Murray and Boutin 1991) and likely escape fishers more easily than porcupines in deep snow. Interestingly, we found that winter precipitation explained more variability in porcupine survival than snowfall alone (89 vs. 53%). We hypothesize that this occurred due to snow penetrability (determined by snow density and the presence–absence of ice crusts) rather than the snow depth itself affecting the relationship between fishers, hares, and porcupines. Winter precipitation, which includes rain and snow, may be a better indicator of snow penetrability than snowfall alone.

Overall, we show a clear association between winter precipitation, porcupine winter survival, and population growth rate. In addition, our examination of the timing and causes of mortality revealed that predation rates were strongly related to snow conditions: porcupine survival probability was the lowest in winter 2004, and this was also a winter with very large amounts of winter precipitation (i.e., the largest since 1994; see S6 in ESM). Our ongoing porcupine population monitoring, performed annually in May since 2005 (see S6 in ESM), also confirmed that high levels of winter precipitation in 2005, 2006, 2007, and 2008 were concomitant with consistently low porcupine numbers in our study area. The consistency between these results strongly suggests that winter precipitation played an important role in modulating predation rates on porcupines (prediction 4), and that changes in predation rates with snow conditions is an important mechanism by which weather conditions influence porcupine population dynamics in eastern Quebec.

Could changes in porcupine abundance be driven by changes in hare or fisher abundance?

Snowshoe hare abundance is known to undergo 8- to 11-year cycles in many parts of Canada (Keith et al. 1984; Krebs et al. 1995; Krebs 2001). These hare cycles have been associated with fluctuating abundances of various other vertebrates (Bulmer 1974; Boutin et al. 1995), including North American porcupines (Keith and Cary 1991). Based on correlations between the abundances of hares, fishers, and porcupines, Bowman et al. (2006) suggested that porcupine populations may fluctuate in response to changes in hare abundance, changes in fisher abundance, and increased predation on porcupines during the fisher peak. We did not find support for this hypothesis in our study system, because regional indexes of hare and fisher abundance were generally not cyclic (Etcheverry et al. 2005; Poulin et al. 2006) and varied only moderately from 2000 to 2004 (see S6 in ESM), contrary to the growth rate, survival, and mortality factors in our porcupine population. Variations in abundance of hares or fishers in our study area may not be reflected in indices of regional variations, but we spent considerable amounts of time in the field to study porcupines and never observed the obvious signs (Krebs et al. 2001) indicating that hare abundance was going through dramatic changes.

Other mechanistic hypotheses linking weather conditions to porcupine survival

We had predicted that low spring temperature would decrease summer survival of juveniles because young mammals are sensitive to hypothermia (Hull 1973) (see “Introduction”, prediction 1). In addition, low spring temperature can influence winter survival of herbivores (Loison and Langvatn 1998) through reduced primary productivity that in turn influences fall body condition (prediction 2). We found no effect of spring temperature on summer or winter survival rates of porcupines. The very high predation pressure we observed on porcupines, resulting from the sustained high density of fishers in eastern Quebec since the middle of the 1990s (Poulin et al. 2006; see S6 in ESM), could have masked the potentially subtle effects of spring temperature on survival.

Conclusion

We identified the following variables as possibly involved in the relationship between weather conditions and porcupine abundance that was detected through the analysis of long-term time series (Klvana et al. 2004): winter precipitation → snow conditions → predation rate → porcupine winter survival → porcupine abundance. Of course it would be naïve to assume simple linearity with no outside interference in such a long series of cause–effect relationships. In addition, our test would have been stronger if we had also documented a relaxation of predation pressure associated with low winter precipitation and subsequent changes in porcupine population abundance. One difficulty associated with studying long ecological cycles (e.g., superimposed 11- and 22-year cycles in local weather conditions) is the challenge of accumulating field data through sufficiently long time periods. However, our small-scale, mechanistic study did generate support for some of the most important links in this potential chain of causes and effects.

Here, we add to the growing body of evidence supporting an effect of climate on predator–prey processes. Our results strongly emphasize that understanding how species interactions vary according to weather conditions is crucial to properly model how communities will respond to climate change (Schmitz 2003; Wilmers and Getz 2005; Sala 2006). In addition, this study highlights that our capability to project the future trajectory of populations under a new climate is limited (Berteaux and Stenseth 2006), except perhaps in simple, albeit rare, situations where interactions between species are limited and dependence of population dynamics on climate is strong.

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References

Berteaux D, Stenseth NC (2006) Measuring, understanding and projecting the effects of large-scale climatic variability on mammals. Clim Res 32:95–97

Berteaux D, Klvana I, Trudeau C (2005) Spring-to-fall mass gain in a northern population of North American porcupines. J Mammal 86:514–519

Berteaux D, Humphries MM, Krebs CJ, Lima M, McAdam AG, Pettorelli N, Reale D, Saitoh T, Tkadlec E, Weladji RB, Stenseth NC (2006) Constraints to projecting the effects of climate change on mammals. Clim Res 32:151–158

Boutin S, Krebs CJ, Boonstra R, Dale MRT, Hannon SJ, Martin K, Sinclair ARE (1995) Population-changes of the vertebrate community during a snowshoe hare cycle in Canada boreal forest. Oikos 74:69–80

Bowman J, Donovan D, Rosatte RC (2006) Numerical response of fishers to synchronous prey dynamics. J Mammal 87:480–484

Bulmer MG (1974) A statistical analysis of the 10-year cycle in Canada. J Anim Ecol 43:701–718

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York

Charlesworth B (1994) Evolution in age-structured populations, 2nd edn. Cambridge University Press, Cambridge

Choquet R, Reboulet A-M, Pradel R, Gimenez O, Lebreton J-D (2003) User's manual for U-CARE, Mimeographed document, CEFE/CNRS, Montpellier (ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR)

Choquet R, Reboulet A-M, Pradel R, Gimenez O, Lebreton JD (2004) M-SURGE: new software specifically designed for multistate capture recapture models. Anim Biodivers Conserv 27:207–215

Cook JG, Irwin LL, Bryant LD, Riggs RA, Thomas JW (1998) Relations of forest cover and condition of elk: a test of the thermal cover hypothesis in summer and winter. Wildl Monogr 141:5–61

Crespin L, Verhagen R, Stenseth NC, Yoccoz NG, Prevot-Julliard AC, Lebreton JD (2002) Survival in fluctuating bank vole populations: seasonal and yearly variations. Oikos 98:467–479

Eberhardt LL (2002) A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854

Etcheverry P, Crete M, Ouellet JP, Rivest LP, Richer MC, Beaudoin C (2005) Population dynamics of snowshoe hares in relation to furbearer harvest. J Wildl Manage 69:771–781

Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toigo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31:367–393

Gauthier G, Pradel R, Menu S, Lebreton JD (2001) Seasonal survival of Greater Snow Geese and effect of hunting under dependence in sighting probability. Ecology 82:3105–3119

Haim A, van Aarde RJ, Skinner JD (1992) Burrowing and huddling in newborn porcupine: the effect on thermoregulation. Physiol Behav 52:247–250

Halfpenny JC, Ozanne RD (1989) Winter, an ecological handbook. Johnson, Boulder

Hebblewhite M (2005) Predation by wolves interacts with the North Pacific Oscillation (NPO) on a western North American elk population. J Anim Ecol 74:226–233

Huggard DJ (1993) Effect of snow depth on predation and scavenging by grey wolves. J Wildl Manage 57:382–388

Hull D (1973) Thermoregulation in young mammals. In: Whittow GC (ed) Comparative physiology of temperature regulation. Special aspects of thermoregulation, vol 3. Academic, New York, pp 167–200

Jedrzejewski W, Schmidt K, Theuerkauf J, Jedrzejewska B, Selva N, Zub K, Szymura L (2002) Kill rates and predation by wolves on ungulate populations in Bialowieza Primeval Forest (Poland). Ecology 83:1341–1356

Keith LB, Cary JR (1991) Mustelid, squirrel, and porcupine population trends during a snowshoe hare cycle. J Mammal 72:373–378

Keith LB, Cary JR, Rongstad OJ, Brittingham MC (1984) Demography and ecology of a declining snowshoe hare population. Wildl Monogr 90:1–43

Klvana I, Berteaux D, Cazelles B (2004) Porcupine feeding scars and climatic data show ecosystem effects of the solar cycle. Am Nat 164:283–297

Krebs CJ (2001) What drives the 10-year cycle of snowshoe hares? Bioscience 51:25–35

Krebs CJ, Berteaux D (2006) Problems and pitfalls in relating climate variability to population dynamics. Clim Res 32:143–149

Krebs CJ, Boutin S, Boonstra R, Sinclair ARE, Smith JNM, Dale MRT, Martin K, Turkington R (1995) Impact of food and predation on the snowshoe hare cycle. Science 269:1112–1115

Krebs CJ, Boutin S, Boonstra R (2001) Ecosystem dynamics of the boreal forest: the Kluane project. Oxford University Press, New York

Langvatn R, Albon SD, Burkey T, Clutton-Brock TH (1996) Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. J Anim Ecol 65:653–670

Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118

Lima M, Stenseth N, Jaksic FM (2002) Population dynamics of a South American rodent: seasonal structure interacting with climate, density dependence and predator effects. Proc R Soc Lond B 269:2579–2586

Lindstrom ER, Hornfeldt B (1994) Vole cycles, snow depth and fox predation. Oikos 70:156–160

Loison A, Langvatn R (1998) Short- and long-term effects of winter and spring weather on growth and survival of red deer in Norway. Oecologia 116:489–500

Loison A, Gaillard JM, Houssin H (1994) New insight on survivorship of female chamois (*Rupicapra rupicapra*) from observation of marked animals. Can J Zool 72:591–597

Morin P, Berteaux D, Klvana I (2005) Hierarchical habitat selection by North American porcupines in southern boreal forest. Can J Zool 83:1333–1342

Murray DL, Boutin S (1991) The influence of snow on lynx and coyote movements—does morphology affect behavior? Oecologia 88:463–469

Owen-Smith N, Mason DR, Ogutu JO (2005) Correlates of survival rates for 10 African ungulate populations: density, rainfall and predation. J Anim Ecol 74:774–788

Patterson BR, Benjamin LK, Messier F (1998) Prey switching and feeding habits of eastern coyotes in relation to snowshoe hare and white-tailed deer densities. Can J Zool 76:1885–1897

Post E, Stenseth NC (1999) Climatic variability, plant phenology, and northern ungulates. Ecology 80:1322–1339

Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystem consequences of wolf behavioural response to climate. Nature 401:905–907

Poulin JF, Jolicoeur H, Canac-Marquis P, Larivière S (2006) Investigation sur les facteurs à l'origine de la hausse de la récolte de pékans (*Martes pennanti*) au Québec depuis 1984. Ministère des Ressources Naturelles et de la Faune, Direction du développement de la faune et Université du Québec à Rimouski, Département de biologie et des sciences de la santé, Quebec (in French)

Powell RA (1993) The fisher. University of Minnesota Press, Minneapolis

Root TL, Schneider SH (1995) Ecology and climate—research strategies and implications. Science 269:334–341

Roze U (1984) Winter foraging by individual porcupines. Can J Zool 62:2425–2428

Roze U (2009) The North American porcupine, 2nd edn. Cornell University Press, Ithaca

Saether BE, Sutherland WJ, Engen S (2004) Climate influences on avian population dynamics. Adv Ecol Res 35:185–209

Sala E (2006) Top predators provide insurance against climate change. Trends Ecol Evol 21:479–480

Sandvik H, Coulson T, Saether BE (2008) A latitudinal gradient in climate effects on seabird demography: results from interspecific analyses. Glob Chang Biol 14:703–713

Schemper M (1990) The explained variation in proportional hazards regression. Biometrika 77:216–218

Schmitz O (2003) Ecosystem responses to global climate change: moving beyond color mapping. Bioscience 53:1199–1205

Sinclair ARE, Gosline JM, Holdsworth G, Krebs CJ, Boutin S, Smith JNM, Boonstra R, Dale M (1993) Can the solar cycle and climate synchronize the snowshoe hare cycle in Canada? Evidence from tree rings and ice cores. Am Nat 141:173–198

Sokal RR, Rohlf FJ (1981) Biometry, 2nd edn. Freeman, New York

Stefan CI, Krebs CJ (2001) Reproductive changes in a cyclic population of snowshoe hares. Can J Zool 79:2101–2108

Stenseth NC, Chan K-S, Tong H, Boonstra R, Boutin S, Krebs CJ, Post E, O'Donoghue M, Yoccoz NG, Forchhammer MC, Hurrell JW (1999) Common dynamic structure of Canada lynx populations within three climatic regions. Science 285:1071–1073

Stenseth NC, Shabbar A, Chan KS, Boutin S, Rueness EK, Ehrich D, Hurrell JW, Lingjaerde OC, Jakobsen KS (2004) Snow conditions may create an invisible barrier for lynx. Proc Natl Acad Sci USA 101:10632–10634

Sweitzer RA (1996) Predation or starvation: consequences of foraging decisions by porcupines (*Erethizon dorsatum*). J Mammal 77:1068–1077

Telfer ES, Kelsall JP (1984) Adaptation of some large North American mammals for survival in snow. Ecology 65:1828–1834

Thibault I, Ouellet JP (2005) Hunting behaviour of eastern coyotes in relation to vegetation cover, snow conditions, and hare distribution. Ecoscience 12:466–475

Tsiropoula G (2003) Signatures of solar activity variability in meteorological parameters. J Atmos Sol Terr Phys 65:469–482

Wilmers CC, Getz WM (2005) Gray wolves as climate change buffers in Yellowstone. Plos Biol 3:0571–0576

Predation as a probable mechanism relating winter weather to population dynamics in a North American porcupine population

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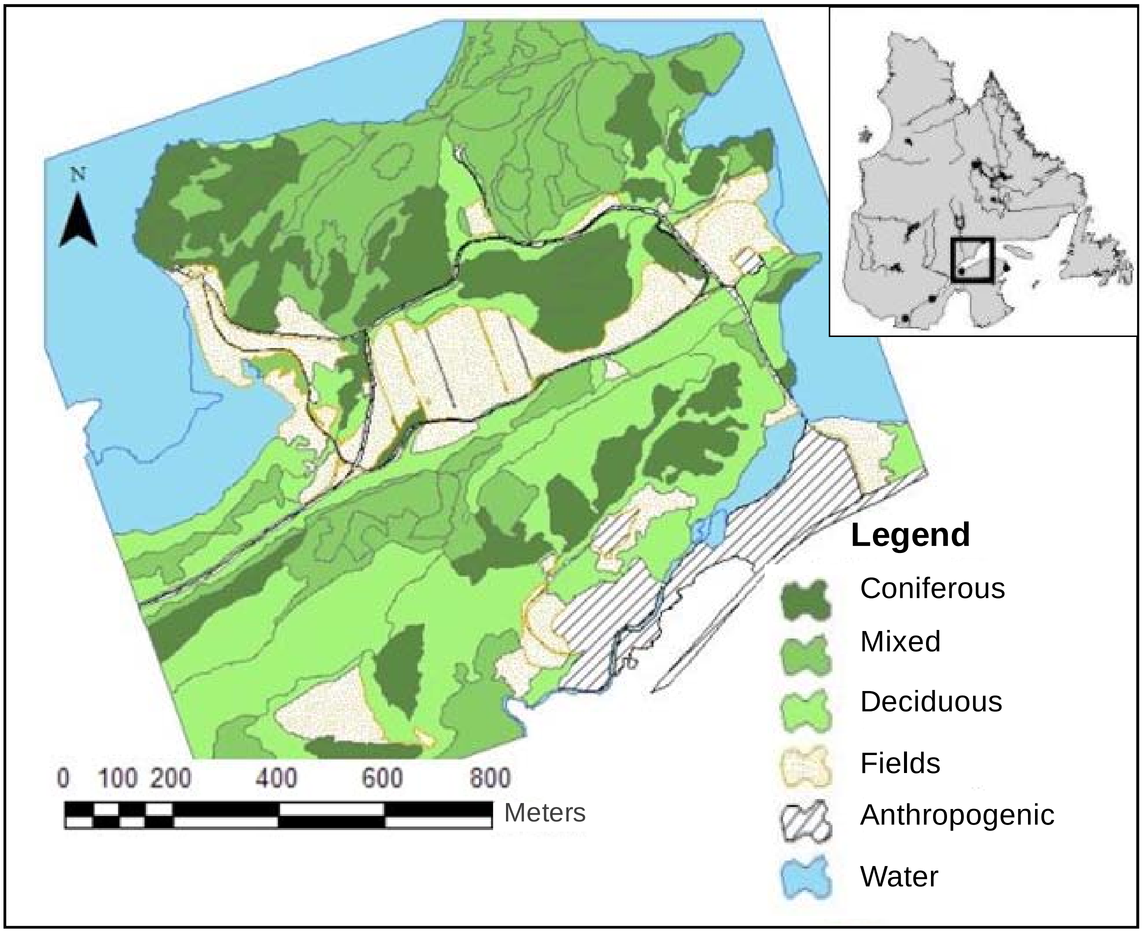
S1: Map of the study area where North American porcupines were followed, Parc National du Bic, Quebec, Canada, May 2000-May 2005.



S2: Annual monitoring effort for a North American porcupine population in Parc National du Bic, Quebec, Canada, May 2000-May 2005. **Survey** gives the number of nights and person-hours spent searching for porcupines within the study area. **Radio-tracking** gives measures of the effort made to radiotrack porcupines (number of individuals radiotracked, proportion of marked individuals radiotracked, and average number of days (± SE) each radiotracked porcupine wore a radiocollar). Note that virtually all adults in the study population were marked.

	2000	2001	2002	2003	2004	2005
Survey						
May[†]						
nights	20[‡]	20[‡]	26	20	22	18
person-hours	150[‡]	150[‡]	481	195	319	225
August						
nights	15[‡]	14	14	5	12	0
person-hours	100[‡]	152	153	69	140	0
Radio-tracking						
Summer (May to August)						
N	12	51	13	38	23	0
% of marked individuals	10.3	60.7	19.7	86.4	100	0
days per individual ± SE	29 ± 6	62 ± 5	62 ± 10	91 ± 7	79 ± 10	0
Winter (August to May)						
N	21	0	19	38	15	0
% of marked individuals	18.0	0	28.8	86.4	65.2	0
days per individual ± SE	54 ± 6	0	147 ± 15	186 ± 10	162 ± 13	0

[†]: 'May' captures sometimes extended into early June to maximize the probability of capture of juveniles; [‡]: these are minimum estimates because precise records of searching effort were initiated in August 2001

S3: Model selection for resighting probabilities (p) in a population of North American porcupines, Parc National du Bic, Quebec, Canada, May 2000-May 2005. We used data on 159 individuals. We considered survival rate to be time-dependent (ϕ_t) in all models and tested for an effect of sex, age (*a*, considering two age classes: juveniles and ≥ 1 yr-old), season (*s*), and year (*y*) on resighting probabilities.

The selected model (bolded) includes an effect of the season, with resighting probability being generally higher in May (0.92 ± 0.03) when porcupines fed quasi-exclusively in fields, than in August (0.70 ± 0.10) when they foraged in fields and forests. Also, resighting probability was constant in May and exhibited yearly variations in August (range: 0.43 in 2002 to 1 in 2004), likely because many resightings in August were of radiocollared porcupines, and our radio tracking effort varied from year to year (S1 in ESM).

Biological meaning	Notation[†]	Deviance	np[$]	ΔAICc[§]
Year effect in summer only	$\mathbf{p^{U}_{y}\,p^{W}}$	**811.193**	**16**	**0.000**
Additive effect of year and season	p_{y+s}	813.622	16	2.429
Effect of time[‡]	p_{t}	807.436	19	3.880
Additive effect of time[‡] and age	p_{t+a}	803.149	21	4.870
Additive effect of time[‡] and sex	$p_{t+\mathrm{sex}}$	807.266	21	8.987
Year effect in winter only	$p^{U}\,p^{W}_{y}$	828.270	16	17.077
Effect of year	p_{y}	859.200	15	45.533
Constant sighting probability	p	869.156	11	45.928

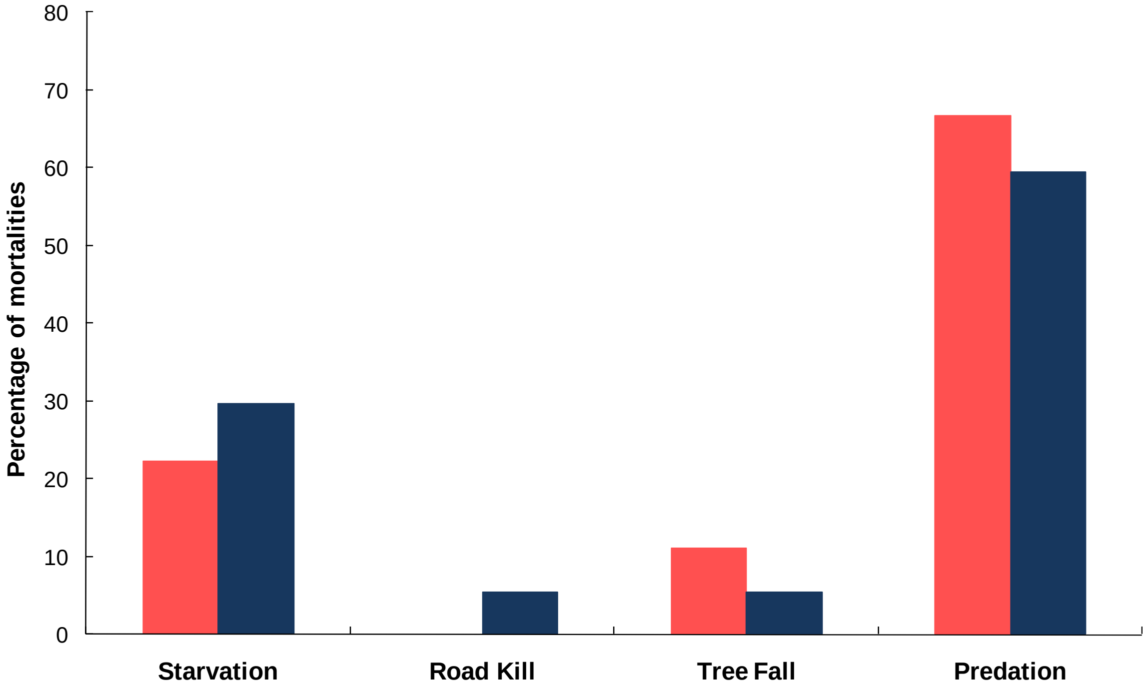
[†]: U, summer; W, winter; [$]: np, number of estimated parameters; [§]: ΔAICc, difference in AICc from the selected model; [‡]: effect of time *t* is equivalent to a *y.s* effect

S4: Tests of lagged effects (one year: *y*-1; two years: *y*-2) of local weather variables on winter survival rates (ϕ^{W}) in a population of North American porcupines, Parc National du Bic, Quebec, Canada, May 2000-May 2005. We used data on 159 individuals. The top model (i.e., most supported by the data) is bolded.

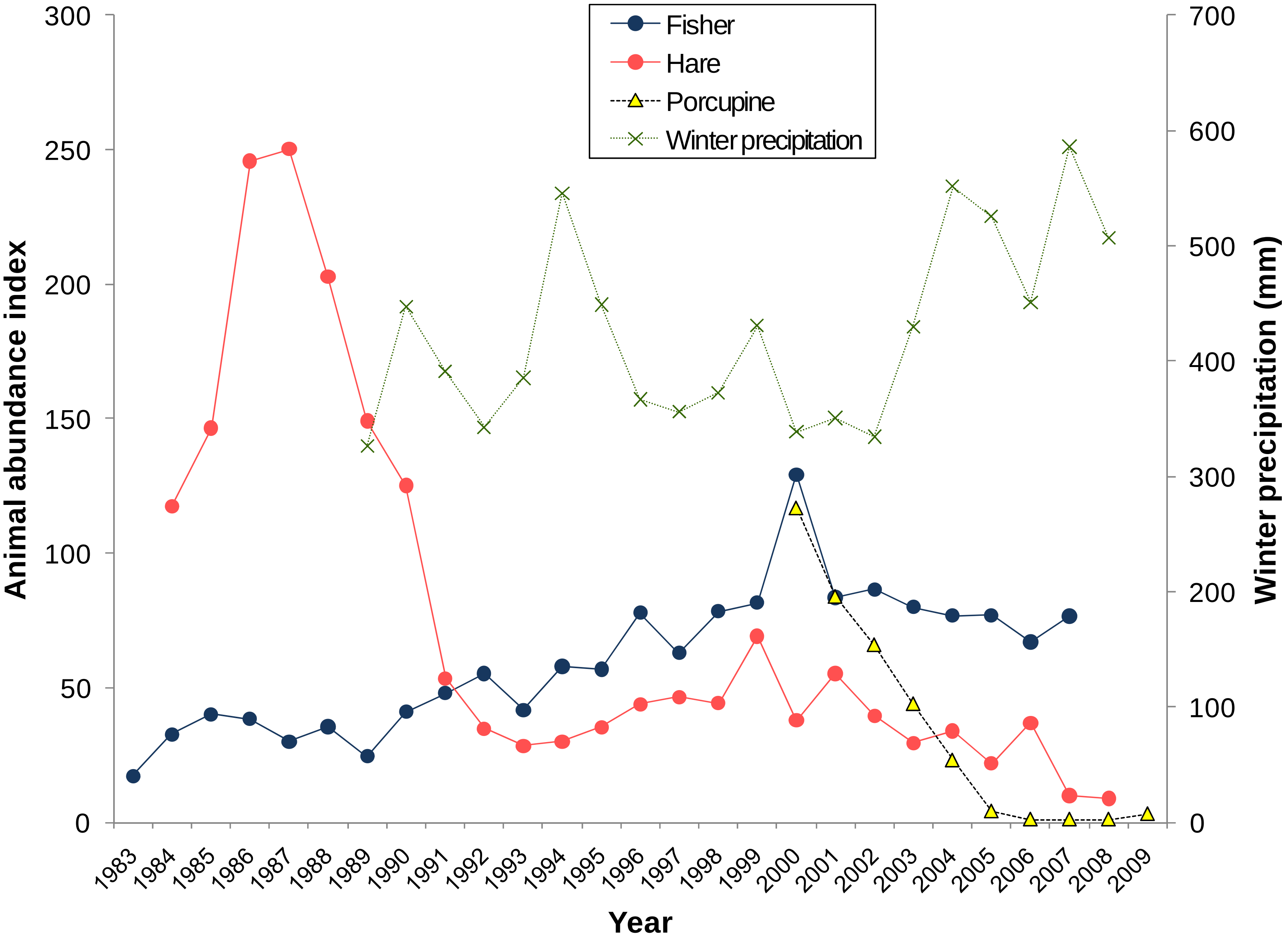
Biological meaning	Notation[†]	Deviance	np[$]	ΔAICc[§]
Direct effect of precipitations, and age effect, *from Table 4*	$\boldsymbol{\phi^{U}_{a}\ \phi^{W}_{\text{Precipitations} + a}}$	**791.309**	**10**	**0.000**
Lagged effect of precipitations (*y*-2), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Precipitations } (y\text{-}2) + a}$	799.045	10	7.736
Lagged effect of snowfall (*y*-1), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Snowfall } (y\text{-}1) + a}$	799.897	10	8.588
Lagged effect of spring temperature (*y*-2), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Spring } (y\text{-}2) + a}$	800.627	10	9.318
Lagged effect of snowfall (*y*-2), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Snowfall } (y\text{-}2) + a}$	800.921	10	9.612
Lagged effect of spring temperature (*y*-1), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Spring } (y\text{-}1) + a}$	802.307	10	10.998
Lagged effect of precipitations (*y*-1), and age effect	$\phi^{U}_{a}\ \phi^{W}_{\text{Precipitations } (y\text{-}1) + a}$	802.314	10	11.005

[†]: U, summer; W, winter; *y*, year; *a*, age modelled as two age classes (juveniles, ≥ 1 yr-old); [$]: np, number of estimated parameters;
[§]: ΔAICc, difference in AICc from the selected model

S5: Causes of mortality for juveniles (*n* = 9, red bars) and individuals ≥ 1 yr-old (*n* = 37, blue bars) found dead in a population North American porcupines, Parc National du Bic, Quebec, Canada, May 2000-April 2005.



S6: Abundance indexes of hares, fishers and North American porcupines in the Lower St-Lawrence region, Quebec, Canada, 1983-2009. The hare index corresponds to the annual number of hares (divided by 10) collected by small game hunters in Wildlife Reserves and Zones of Controlled Exploitation of the region (source: MRNF- Direction Régionale du Bas-St-Laurent). The fisher index corresponds to the number of fisher pelts (divided by 10) traded by trappers via the regional fur trade control system (source: MRNF website: http://www.mrnf.gouv.qc.ca/faune/statistiques/chasse-piegeage.jsp). The fisher abundance index for year *t* corresponds to the number of pelts traded in year *t*+1. The porcupine index corresponds to the minimum number of porcupines found to be alive each May in Parc National du Bic. This spring census involved ≥ 80 person-hours of field work per year. Winter precipitation (mm) for year *t* corresponds to total precipitation from November (year *t*) to April (year *t*+1) measured at the Rimouski Environment Canada weather station (approximately 20 km from our study site), Quebec, Canada, 1989-2008. The precipitation time series starts in 1989 because of incomplete data for the 1983-1988 period.



Mabille et al. S6.