Journal of Mammalogy, 86(3):514–519, 2005

SPRING-TO-FALL MASS GAIN IN A NORTHERN POPULATION OF NORTH AMERICAN PORCUPINES

DOMINIQUE BERTEAUX,* ILYA KLVANA, AND CAROLINE TRUDEAU

Canada Research Chair in Conservation of Northern Ecosystems and Centre d'Études Nordiques,
Université du Québec à Rimouski, 300 allée des Ursulines, Rimouski, Québec G5L 3A1, Canada

Mammalian herbivores from northern environments often store fat in summer to decrease the energetic stress of winter. We measured mass gain during the spring-to-fall season in a Quebec population of North American porcupines (*Erethizon dorsatum*) and determined how it is affected by the age, sex, and reproductive status of individuals. Porcupines gained mass without interruption from midspring to late summer, but mass gains were more important in mid- to late spring and late summer than at other times. This likely reflected local variations in the nutrient content of forage. Adult males lost mass during the rutting period of early fall. All age–sex classes except lactating females gained about 3 kg, or 40% of their spring body mass. This is not markedly different from mass gains observed in other nonhibernating mammalian herbivores. We generate the hypothesis that in this population some ecological, behavioral, or physiological mechanism limits the rate of mass increase to about 21 g per day.

Key words: energy, *Erethizon dorsatum*, fat, herbivores, mass gain, northern environment, porcupine, seasonality, weight, winter

Mammalian herbivores living in northern environments face a strong seasonality in food availability and energetic costs of thermoregulation (Halfpenny and Ozanne 1989; Marchand 1991). As a result, they have evolved ways of accumulating energy during the summer and fall seasons in the form of fat or food stores. These stores are later used to reduce the energetic deficit of winter. How much energy is stored before winter is critical because it directly affects the probability of survival to the next spring.

Vegetation contains low amounts of digestible energy (Robbins 1993) and is difficult to conserve over the long term. Therefore, mammalian herbivores usually store fat instead of food (pikas and beavers are among the rare exceptions—Busher 1996; Dearing 1997). Understanding what limits the amounts of fat stored before winter is a key aspect of understanding the winter ecology of mammalian herbivores.

The upper limit to fat storage could be set by food availability, the rate of food acquisition, the rate of transformation of food into fat, and the fat-storage capacity of individuals. Most of these limiting sources can have various proximate and ultimate causes. For example, the fat-storage capacity of individuals can be limited by proximate reasons such as the skeletal constraints to maximal body volume, or by ultimate reasons such as the need to efficiently run away from predators. In order to make progress in our understanding of the factors limiting summer fat storage in mammals from seasonal environments, we clearly need data on patterns of fat storage from a variety of species differing in life-history characteristics.

Here we use information from a population of individually marked North American porcupines (*Erethizon dorsatum*) to examine spring-to-fall mass gain in a mammalian herbivore living in a strongly seasonal environment. Sweitzer and Berger (1993) described the winter mass decrease in a porcupine population and showed that substantial mass loss and high rates of starvation occur in this species (see also Roze 1984, 1989). However, no published data exist on the dynamics of spring-to-fall mass gains, perhaps because porcupines are elusive and usually difficult to capture in large numbers in summer.

In this paper we describe porcupine mass gain during the spring-to-fall season. First, we quantify the progression of porcupine mass gain through time and determine how it is affected by the age, sex, and reproductive status of individuals. Second, we quantify the overall spring-to-fall porcupine mass gain for each age–sex–reproductive status class in order to generate data comparable to previously published estimates of summer mass gain. Third, we compare our findings to those from other nonhibernating mammalian herbivores.

MATERIALS AND METHODS

Field data collection.—We studied a population of individually marked porcupines in an ~2-km^2 area of Parc National du Bic (48°21′N, 68°46′W, elevation 0–150 m), Québec, Canada. We collected mass data from early May to mid-November in 2000 and 2002, and from early May to late August in 2001. The study area is

---

* *Correspondent: dominique_berteaux@uqar.qc.ca*

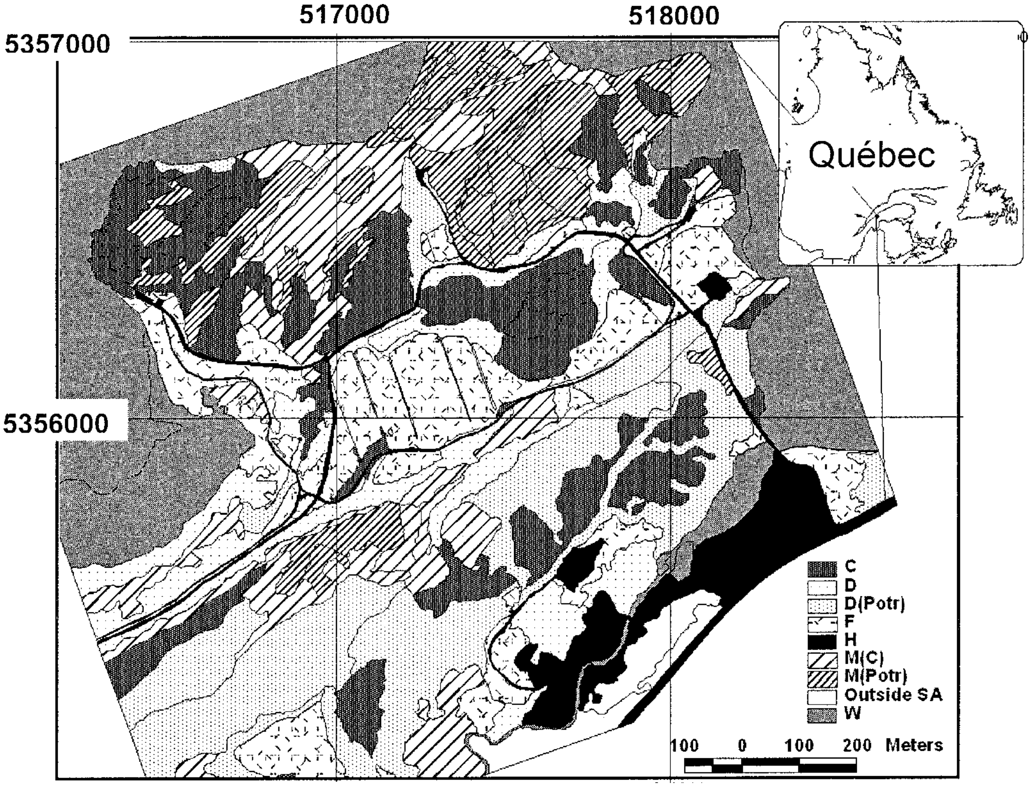

Fig. 1.—Study area in Parc National du Bic, Québec, Canada (48°21′N, 68°46′W) and main habitat types available to porcupines. Habitat types: C = conifer forest, D = deciduous forest, D(POTR) = trembling aspen–dominated deciduous forest, F = fields, H = human-used land (mostly roads and buildings), M = mixed forest, M(POTR) = trembling aspen–dominated mixed forest. Grid gives Universal Transverse Mercator (UTM) coordinates (zone 19N), habitat type "W" indicates water bodies (St. Lawrence River), and habitat type "Outside SA" indicates habitats outside of the study area.

characterized by a rugged topography, abundance of natural rock dens, and a mixed-boreal forest dominated (in order of importance) by trembling aspen (*Populus tremuloides*), eastern white cedar (*Thuya occidentalis*), white spruce (*Picea glauca*), and balsam fir (*Abies balsamea*; Fig. 1). The area is fragmented by abandoned and cultivated fields. The climate is characterized by cold winters and mild summers (Fig. 2). Precipitation is relatively abundant and distributed uniformly throughout the year (total annual precipitation = 1,005.3 mm; Fig. 2). The most difficult period for porcupines is November through April, because vegetation is dormant and most precipitation falls in the form of snow, usually covering the ground through most of this period (Fig. 2). We quantified the phenology of vegetation by measuring every spring (2000–2002) the length of a sample of leaves from trembling aspen, white birch, and white spruce trees. In addition, we also noted timing of green up of ground vegetation (mostly graminoids) in a few abandoned fields located in the study area.

We captured porcupines during night patrols (by foot or bicycle) of the study area. We usually restricted patrols to open areas (trails, roads, and cultivated and old fields) and adjacent forested areas, because porcupines were easier to locate in these habitats. We located porcupines by sight by using spotlights (Model Q-Beam Max Million, The Brinkmann Corporation, Dallas, Texas), or by sound when animals were traveling on the ground or feeding in a tree. Porcupines found on ground or low in trees or shrubs were captured in a dip net. Once captured, we used a drawcord to close the net and retain the animal for manipulations. We forced porcupines found in a tree to descend by agitating a pole above the animal. If this was impossible (tree too high) or unsuccessful, we strapped 3 or 4 single-door live traps (82 × 27 × 33 cm, Tomahawk Live Trap Company, Tomahawk, Wisconsin) vertically to the tree trunk so that the porcupine could only descend into one of the traps. We checked traps 2–12 h later. When the porcupine had been caught it was transferred to a dip net for manipulations. In rare occasions, we climbed the tree to capture the porcupine, but we avoided this approach for the safety of both porcupines and field workers.

We weighed porcupines in the dip net with a spring scale (Pesola Macro Line 10 kg or 20 kg, Pesola AG, Baar, Switzerland) and anesthetized untagged individuals with a mixture of ketamine hydrochloride (5 mg/kg) and xylazine hydrochloride (2 mg/kg) injected in the tail muscles (Morin and Berteaux 2003). Once anesthetized, porcupines were sexed, measured, and ear-tagged with a unique combination of 2 color- and sign-coded plastic tags (15 × 45 mm cut out of plastic cattle tags, Allflex USA, Inc., Dallas Ft. Worth Airport, Texas) attached to the bottom part of the ears by using self-piercing aluminium ear tags (tag size 3, National Band and Tag Co., Newport, Kentucky). In addition, 2 smaller self-piercing aluminium ear tags (tag size 3, National Band and Tag Co.) were attached to the upper part of the ears to maintain an individual's identity in case both larger plastic tags were lost. We determined reproductive status of females (pregnant, lactating, or nonreproductive) by palpation of the abdomen (pregnancy) or by attempting to extract milk from 1 or several nipples (lactation).

Each individual was classified according to sex and age (juvenile, subadult, or adult). Juveniles were easy to identify based on small body size. Subadults were differentiated from adults based on body mass in May. Females weighing less than 4.5 kg and males weighing less than 5 kg were considered to be subadults. Examination of data from juveniles or subadults recaptured in the following year confirmed that these age classification criteria were accurate. Because the energy invested in lactation likely has an impact on mass gain, adult females were classified as lactating if they were observed to be lactating at least once in a given summer and as nonreproductive if there was no evidence of lactation during that year. Reproductive status was not considered in adult males because all were probably involved in the fall mating period (Roze 1989). Because only adult females could be lactating and because there were very few data for juvenile females, the 3 age, sex, and reproductive status variables were condensed into

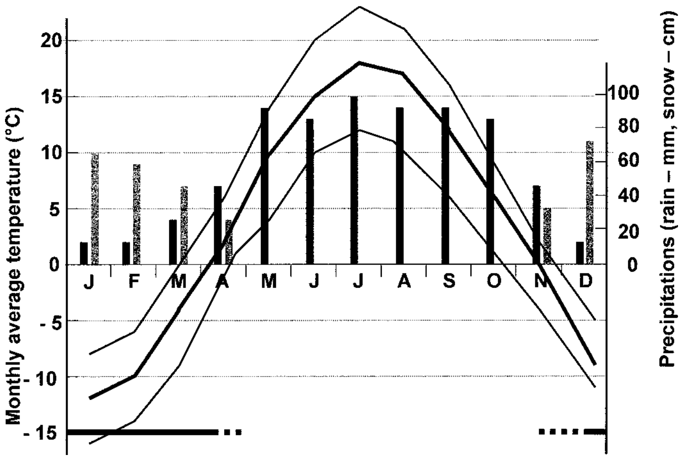

FIG. 2.—Meteorological data at Parc National du Bic, Québec, Canada. Vertical bars represent monthly average precipitation (black bars = water in millimeters, gray bars = snow in centimeters), curves represent monthly maximum, average, and minimum temperatures (daily averages), and horizontal thick line represents times of permanent (solid line) or intermittent (dotted line) snow cover. Meteorological data are averages for the period 1971–2000 (weather station of Rimouski, located 25 km east of the study area).

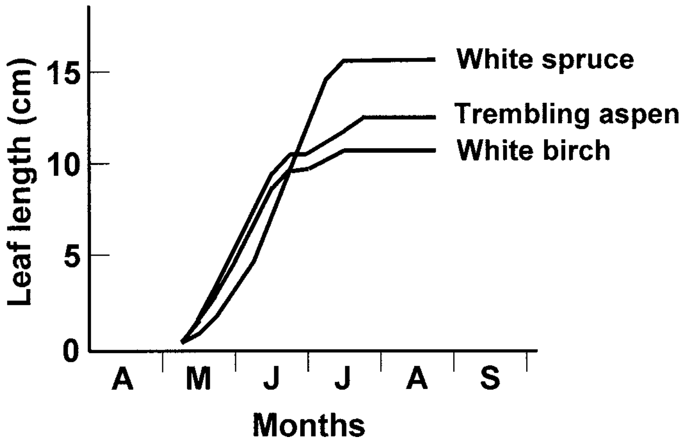

FIG. 3.—Spring and summer plant phenology (bud or leaf length for representative tree species) at Parc National du Bic, Québec, Canada. Transformation of buds into leaves occurred on 27 May, 24 May, and 13 May for white spruce, trembling aspen, and white birch, respectively. Plant phenological data are averages for the period 2000–2002 (data collected at the study area).

a single age–sex–status variable with the following classes: juveniles, subadult males, subadult females, adult males, lactating adult females, and nonreproductive adult females. Capture techniques and immobilization procedures followed guidelines of the American Society of Mammalogists (Animal Care and Use Committee 1998) and were approved by the McGill Animal Care Committee (permit 4213), the Comité de protection des animaux de l'Université du Québec à Rimouski (permit CPA12-02-06), and the Société de la Faune et des Parcs, Gouvernement du Québec (permits 20000417-001-01-S-P to 20020401-001-01-S-F).

Data analyses.—Data from individuals weighed in several years were considered independent, so all analyses are based on "individual-years." When an individual had been weighed twice or more within 5 consecutive days, the masses were averaged and assigned to the average date.

In order to allow comparison of masses and rates of mass change between different periods of the year and between different age–sex–status classes, we used linear interpolation and extrapolation to estimate the mass of individuals at 8 specific dates spaced 4 weeks (28 days) apart: day 2 (2 May), day 30 (30 May), day 58 (27 June), day 86 (25 July), day 114 (22 August), day 142 (19 September), day 170 (17 October), and day 198 (14 November). Estimates were only generated if an actual mass had been recorded within 14 days of these dates. We used linear extrapolation to estimate a mass only if we had recorded 2 successive masses $\geq$ 14 days apart. A total of 697 estimated masses were obtained from 146 individuals representing 206 individual-years.

The mass change of each individual during each 28-day period was calculated whenever 2 consecutive mass estimates were available for the same individual. Periods of mass change were: midspring (2–30 May), late spring (30 May–27 June), early summer (27 June–25 July), midsummer (25 July–22 August), late summer (22 August–19 September), and early fall (19 September–17 October). The effect of period and age–sex–status class on mass change was analyzed by using a 2-way analysis of variance (ANOVA). Fisher's least significant difference post hoc test was used to detect differences among age–sex–status classes within the same period and among periods within the same age–sex–status class. Mass changes that occurred during midfall (17 October–14 November) were excluded from the analysis because only data on adult and subadult males were available. Data on juveniles also were excluded from the ANOVA because no juvenile data were available during midspring (most juveniles are born in mid- to late May). A total of 397 mass changes from 100 individuals representing 157 individual-years were included in the ANOVA.

When calculating mass gains over the entire season (2 May–17 October), we could not use individual gains because only a few animals had been weighed both at the beginning and at the end of the season. Instead, we added the average gains for all periods for each age–sex–status class. We judged this method to be more accurate than calculating mass gain based on average mass at the beginning and end of the season because these averages would not have been based on the same individuals. Results are reported as means ± *SE*.

RESULTS

Growth of tree leaves started in mid-May in our study area, with most of the leaf growth occurring in June (Fig. 3). By mid-July tree leaves had reached their asymptotic size (Fig. 3). Green up of graminoids in abandoned fields started in the 1st days of May.

Progression of summer mass gain.—Porcupine mass gain depended on period ($F = 6.35$, $d.f. = 5, 371$, $P < 0.001$) and on the interaction between period and age–sex–status class ($F = 2.97$, $d.f. = 20, 371$, $P < 0.001$; Table 1; Fig. 4A). When all age–sex–status classes are considered together, mass gain was highest during mid- and late spring (2 May–27 June) and late summer (22 August–19 September), moderate during early and midsummer (27 June–22 August), and null during early fall (19 September–17 October; Table 1; Fig. 4A). In other words, porcupines gained mass without interruption from midspring to late summer, but mass gains were significantly more important in mid- to late spring and late summer than at other times.

TABLE 1.—Mass gains (kg) for 5 age–sex–status classes of porcupines during six 28-day periods. Sample sizes are in porcupine-years. Letters indicate significance of differences between groups: identical lowercase letters (to be read across rows) indicate nonsignificant differences in mass gains for different classes within the same period; identical uppercase letters (to be read down columns) indicate nonsignificant differences in mass gains for different periods within the same class. Data are for 2000–2002, Parc National du Bic, Québec, Canada.

	Adult males		Adult lactating females		Adult non-reproductive females		Subadult males		Subadult females		All classes	
Period	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$
Midspring (2−30 May)	43	0.93 ± 0.07aA	41	0.51 ± 0.07bA	8	0.76 ± 0.13abA	5	0.66 ± 0.16abA	5	0.71 ± 0.10abA	102	0.73 ± 0.05A
Late spring (30 May−27 Jun.)	36	0.80 ± 0.07aA	31	0.58 ± 0.07bA	7	0.59 ± 0.06abA	5	0.82 ± 0.07abA	4	0.65 ± 0.16abA	83	0.70 ± 0.04A
Early summer (27 Jun.−25 Jul.)	30	0.30 ± 0.06aB	33	0.29 ± 0.06aB	5	0.51 ± 0.05aA	5	0.44 ± 0.12aA	2	0.45 ± 0.20aA	75	0.32 ± 0.04BD
Midsummer (25 Jul.−22 Aug.)	28	0.43 ± 0.08aB	28	0.38 ± 0.08aAB	7	0.51 ± 0.14aA	5	0.69 ± 0.07aA	4	0.28 ± 0.28aA	72	0.43 ± 0.05BC
Late summer (22 Aug.−19 Sep.)	13	0.47 ± 0.14aB	10	0.53 ± 0.08aAB	3	0.83 ± 0.03aA	5	0.59 ± 0.12aA	2	0.80 ± 0.25aA	33	0.56 ± 0.07AC
Early fall (19 Sep.−17 Oct.)	16	−0.31 ± 0.13aC	10	0.30 ± 0.18bAB	2	0.68 ± 0.13bA	2	−0.50 ± 0.10aB	2	0.68 ± 0.18bA	32	−0.01 ± 0.11D

When each age–sex class is considered separately, adult males showed the greatest variation in mass gain throughout the season, with the gain being maximal during mid- and late spring, reduced during summer, and negative during early fall (Table 1). Despite a reduced sample size, examination of our data suggests that subadult males followed a similar pattern of mass gain. Although mass gain for subadult males did not differ significantly between periods ranging from midspring to late summer, mass gain during early fall was significantly different from mass gain during other periods and was negative (Table 1). On the other hand, females, whether lactating adults, nonreproductive adults, or subadults, gained mass more uniformly between early May and mid-October. Mass gain of females never attained the maximal mass gain of adult males, but females did not lose mass during any period (Table 1).

Overall summer mass gain.—When mass gains for all 6 periods were cumulated for each age–sex–status class, subadult females and adult nonreproductive females gained substantially more mass (3.56 and 3.87 kg, respectively) than adult lactating females (2.58 kg), adult males (2.62 kg), and subadult males (2.70 kg). When considered only over the early spring to late summer periods (to eliminate the effect of mass loss of males during early fall), these cumulative differences where reduced, except for adult lactating females, which gained substantially less mass then other classes (2.29 kg for adult lactating females versus 3.20, 2.93, 2.89, and 3.20 kg for adult nonreproductive females, adult males, subadult females, and subadult males, respectively).

When cumulative mass gain was considered in relation to average spring mass for each age–sex–status class on 2 May (approximately the annual minimum), adult males and adult lactating females had very similar rates of mass gain (Fig. 4B). Adult males gained 40.3% of their spring mass from early spring to late summer, with the loss during early fall reducing this gain to 36.0% (Fig. 4B). Comparatively, adult lactating females gained 35.0% of their spring mass from early spring to late summer, but caught up with adult males during early fall, gaining 39.8% of their spring mass from early spring to early fall (Fig. 4B). Much higher relative mass gains were achieved over the early spring–early fall period by nonreproductive adult females (66.1%), subadult females (112.7%), and subadult males (71.2%), although sample sizes for these age–sex–status classes were small (Fig. 4B). The marked difference between total mass gain of subadult females and subadult males is again mostly a result of males losing mass during early fall, whereas females were still gaining mass. When only the period from early spring to early fall was considered, subadult males and females gained 84.4% and 91.3% of their spring mass, respectively (Fig. 4B).

DISCUSSION

Progression of summer mass gain.—Observation of plant phenology in our study area shows that porcupine mass gain from midspring to early fall (2 May–17 October) reflects variations in food availability, because fresh and nutrient-rich vegetation appeared in early May, shortly after snowmelt, and was gone for the most part with the 1st heavy frosts of mid-October. For all age–sex–status classes, there was a tendency for maximal mass gain to occur during mid- and late spring (2 May–27 June) and late summer (22 August–19 September), with mass gain being less important during early and midsummer (27 June–22 August). This is most likely the result of changes in the nutrient content of forage throughout the summer. At the onset of the growing season, nutrient content of leaves is generally highest, after which it declines throughout the summer (Roze 1989). During the month of May, porcupines in our study area fed extensively on young shoots of grasses and forbs found in fields and other open areas, providing them with a high-quality, protein-rich diet ideal for rapid mass gain. When tree leaves became available in late May, porcupines switched to a predominantly tree-leaf diet dominated by trembling aspen. They most likely benefited from a young-leaf, high-quality diet until late June. In July and August, the nutrient content of mature leaves was probably lower, leading to a reduced mass gain. However, during late summer (22 August–19 September), other high-quality plant parts became available, because we observed porcupines feeding extensively on grain in barley fields and on fruits of *Amelanchier* and *Sorbus*. This new, high-quality food source was likely responsible for the increased mass gain of porcupines in late summer.

The marked difference in mass gain between males and females during early fall (19 September–17 October) is most probably a result of the energetic and temporal cost of the fall breeding season for males (Roze 1989; Sweitzer 2003), with females still being able to fatten up on fruit, grain, and other high-quality forage. Similar results were found for other mammalian herbivores breeding in the fall, such as moose and deer (Franzmann et al. 1978; Mitchell et al. 1976). Mass loss of males observed during early fall was not restricted to adult males. Subadult males also lost mass, suggesting that they may already have been sexually mature. This is not in agreement with Roze (1989), who found from a small sample size that males become mature at 24 months of age. However, it is possible that subadult males participate in the fall rut without being fully sexually mature.

Overall summer mass gain.—If only the 20-week period extending from midspring to late summer is considered (to eliminate the effect of mass loss of males during early fall), it is noteworthy that all age–sex–status classes, except adult lactating females, gain about 3 kg, regardless of age and sex. This most likely reflects the maximal mass gain that can be achieved by a porcupine when it does not need to invest in reproduction. This allows us to generate the hypothesis that some mechanism limits the rate of summer mass gain to about 21 g/day in this population of porcupines. Further research should test whether this upper limit is of ecological (food availability), behavioral (grazing–browsing time or grazing–browsing efficiency), or physiological (digestion or assimilation) origin.

When overall mass gain is expressed in relation to mass on 2 May, subadults gain a distinctly greater percentage of their initial mass than adults. This could have been expected given their young age, which still allows for structural growth. The greater mass gain of adult nonreproductive females (versus lactating females) may be the result of both the absence of reproductive costs and the fact that some of these females may not yet have attained their adult mass.

The 40% mass gain that we found in breeding adult male and female porcupines from their minimum spring mass to their respective maximum late-summer and early-fall mass is comparable to what has been documented in porcupines and other nonhibernating herbivores. Sweitzer and Berger (1993) found in the Great Basin desert of Nevada that the mass of adult male porcupines oscillated between a maximum of 11.8 kg in October and a minimum of 7.9 kg in March–April, representing a summer gain of 49%. Mass of adult females varied between a maximum of 8.7 kg in October and a minimum of 6.5 kg in March–April, representing a summer mass gain of 34%. Despite the small sample size of Sweitzer and Berger (1993) and the fact that they only obtained data from 15 October to 15 April, these figures are relatively similar to what we obtained.

Comparison with other species.—Festa-Bianchet et al. (1996) reported summer mass gains ranging from 27% to 33% for different age and sex classes of bighorn sheep (*Ovis canadensis*) in Alberta, Canada. However, these values likely underestimate total summer gain (from minimum to maximum), because they reflect mass gain only from 5 June to 15 September. DelGiudice et al. (1992) reported mass gains of 45% for female white-tailed deer (*Odocoileus virginianus*) in Minnesota from their minimum in May to their maximum in October. Summer mass gains of reindeer (*Rangifer tarandus*) on the sub-Antarctic island of South Georgia (Leader-Williams and Ricketts 1981), deduced graphically from a fitted curve with a sine component, were of about 15% for adult females and 30% for adult males. Winter weight loss in Japanese serow (*Capricornis crispus*–Miura and Maruyama 1986) suggests that the complementary summer mass gain is at least 18% in adult males and 20% in adult females, although these figures probably underestimate the total seasonal fluctuation becuase masses were obtained only from November to March. Franzmann et al. (1978) reported summer mass gains of 42% for female Alaskan moose (*Alces alces gigas*) between June and December and 47% for males between June and September. For Scottish red deer (*Cervus elaphus*), Mitchell et al. (1976) found that males gained 31% of their live weight from a minimum in April–May to

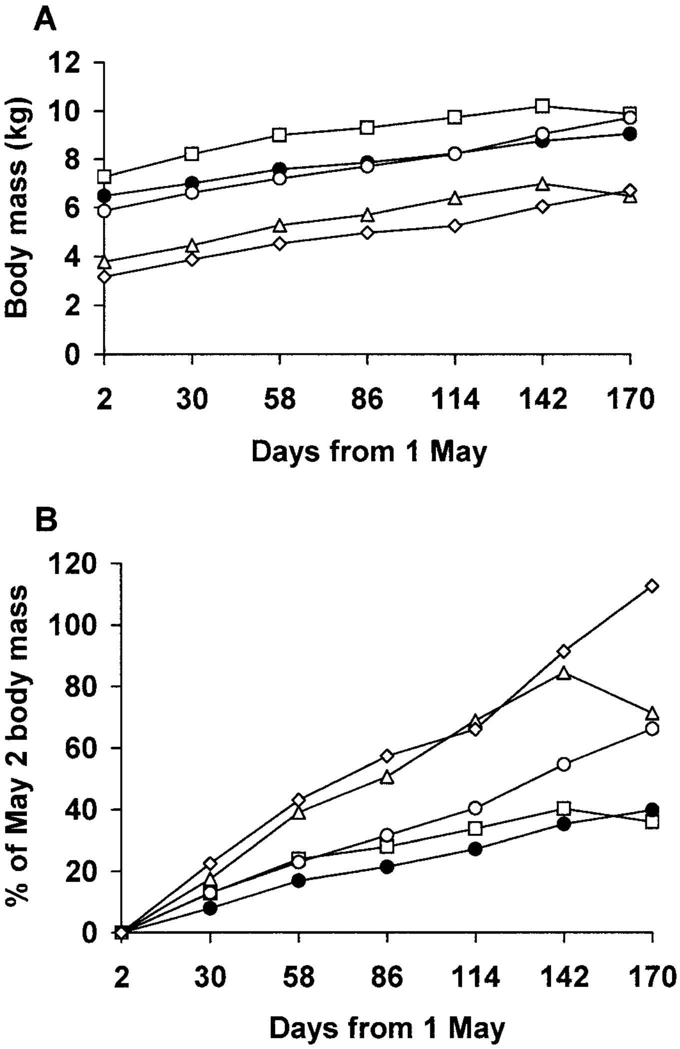

FIG. 4.—A) Body mass trajectories of adult male (open squares), adult lactating female (closed circles), adult nonreproductive female (open circles), subadult male (triangles), and subadult female (diamonds) porcupines in Parc National du Bic, Québec, Canada. Mass trajectories are based on mean estimated body mass of each class on 2 May and on mean estimated gains for each 28-day period and each class. B) Relative mass gain since 2 May.

a maximum in September, just before the rut. Nonlactating females gained 19% of their mass from a minimum in April and May to a maximum in November, with lactating females gaining only 15% during the same period (Mitchell et al. 1976). Therefore, it is reasonable to suspect that a 25–40% seasonal body mass increase is representative of most nonhibernating mammalian herbivores. It must be noted, however, that this does not include small-sized species such as microtine rodents.

One may have expected that porcupines could have gained more mass than other nonhibernating mammalian herbivores because their predator-defense mechanisms might allow them to compromise on agility. However, this hypothesis does not seem to hold, the most likely reason being that porcupines, although having the luxury of compromising on agility on the ground, may not be able to compromise on agility in the trees. There is a strong selective pressure against excessively heavy porcupines, because extra weight while climbing trees leads to increased chances of mortality (Curtis and Kozicky 1944; Hale and Fuller 1996; Marshal 1951; Roze 1989). We have ourselves observed 1 large male porcupine falling off a small trembling aspen when the top of the tree broke under his weight, and have also found several porcupine carcasses that were likely the result of a fatal fall from a tree.

RÉSUMÉ

Les mammifères herbivores des régions nordiques accumulent souvent des réserves de graisse en été pour réduire le stress énergétique de la période hivernale. Nous avons mesuré les gains en masse dans une population de porcs-épics d'Amérique (*Erethizon dorsatum*) du Québec et avons déterminé l'influence de l'âge, du sexe et du statut reproducteur des individus. Les porcs-épics ont continuellement pris du poids du printemps à la fin de l'été, mais les gains les plus importants se sont effectués dans la deuxième moitié du printemps et à la fin de l'été. Cela reflète probablement les variations dans la qualité nutritive de leur alimentation. Les mâles adultes ont perdu du poids pendant la période de rut automnale. Toutes les classes d'âge–sexe, sauf les femelles allaitantes, ont gagné environ 3 kg, ou 40% de leur masse printanière. Ceci n'est pas très différent de ce que l'on observe chez les autres mammifères herbivores non hibernant. Nous générons l'hypothèse qu'il y a dans cette population des mécanismes écologiques, comportementaux, ou physiologiques qui limitent le taux de prise de poids à environ 21 g par jour.

ACKNOWLEDGMENTS

We thank the many field assistants who participated in porcupine captures, and particularly J. Roberge for the formation of field crews and maintenance of camp and field equipment. We thank the personnel from Parc National du Bic for their support during the project. Financial support was provided by the Natural Sciences and Engineering Research Council of Canada, the Fonds Québécois de la Recherche sur la Nature et les Technologies, the Canada Research Chairs Program, and the Canada Foundation for Innovation.

LITERATURE CITED

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 79:1416–1431.

BUSHER, P. E. 1996. Food caching behavior of beavers (*Castor canadensis*): selection and use of woody species. American Midland Naturalist 135:343–348.

CURTIS, J. D., AND E. L. KOZICKY. 1944. Observations on the eastern porcupine. Journal of Mammalogy 25:137–146.

DEARING, M. D. 1997. The function of haypiles of pikas (*Ochotona princeps*). Journal of Mammalogy 78:1156–1163.

DELGIUDICE, G. D., L. D. MECH, K. E. KUNKEL, AND E. M. GESE. 1992. Seasonal patterns of weight, hematology, and serum characteristics of free-ranging female white-tailed deer in Minnesota. Canadian Journal of Zoology (London) 70:974–983.

FESTA-BIANCHET, M., J. T. JORGENSEN, W. J. KING, K. G. SMITH, AND W. D. WISHARD. 1996. The development of sexual dimorphism: seasonal and lifetime mass changes in bighorn sheep. Canadian Journal of Zoology 74:330–342.

FRANZMANN, A. W., R. E. LERESCHE, R. A. RAUSCH, AND J. L. OLDMEYER. 1978. Alaskan moose measurements and weights and measurements–weight relationships. Canadian Journal of Zoology 56:298–306.

HALE, M. B., AND T. K. FULLER. 1996. Porcupine (*Erethizon dorsatum*) demography in central Massachusetts. Canadian Journal of Zoology 74:480–484.

HALFPENNY, J. C., AND R. D. OZANNE. 1989. Winter: an ecological handbook. Johnson Books, Boulder, Colorado.

LEADER-WILLIAMS, N., AND C. RICKETTS. 1981. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. Oikos 38:27–39.

MARCHAND, P. J. 1991. Life in the cold. 2nd ed. University Press of New England, Hanover, New Hampshire.

MARSHAL, W. H. 1951. Accidental death of a porcupine. Journal of Mammalogy 32:221.

MITCHELL, B., D. MCCOWAN, AND A. NICHOLSON. 1976. Annual cycles of body weight and condition in Scottish red deer, *Cervus elaphus*. Journal of Zoology 180:107–127.

MIURA, S., AND N. MARUYAMA. 1986. Winter weight loss in Japanese serow. Journal of Wildlife Management 50:336–338.

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

ROBBINS, C. T. 1993. Wildlife feeding and nutrition, 2nd ed. Academic Press, San Diego, California.

ROZE, U. 1984. Winter foraging by individual porcupines. Canadian Journal of Zoology 62:2425–2428.

ROZE, U. 1989. The North American porcupine. Smithsonian Institution Press, Washington, D.C.

SWEITZER, R. A. 2003. Breeding movements and reproductive activities of porcupines in the Great Basin desert. Western North American Naturalist 63:1–10.

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

Submitted 12 April 2004. Accepted 24 October 2004.

Associate Editor was William L. Gannon.