

Black bear adaptation to low productivity in the boreal forest¹

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Abstract: Long snowy winters combined with a short growing season make boreal forests an unproductive environment that challenges black bears (*Ursus americanus*). We used resource selection functions (based on GPS telemetry of 16 bears), diet analysis, surveys of plant phenology, and vegetation inventories to study adaptations of black bears to boreal forest. Because plants are heavily favoured in bear diets, we expected diet composition to reflect their temporal availability. We anticipated that bears would make choices among land cover types and specific topographic conditions in order to select plants that would fulfil their energetic demands throughout the active period. We also predicted that bears would select habitats modified by insect outbreaks or forest harvesting because these disturbances likely increase resource availability. We found supporting evidence for all of our predictions. (1) Bear diet was closely linked to plant availability. (2) Bears made seasonal altitudinal movements and selected sites according to solar irradiation, tracking the availability of the most digestible plants. Accordingly, bears relied on high-altitude graminoids in spring, a variety of fleshy fruits in summer, and mainly *Sorbus americana* berries in autumn. (3) Land covers resulting from clearcutting and insect outbreaks increased resource availability for bears and were preferred from summer to autumn. In our study area, black bears are considered predators of a threatened caribou (*Rangifer tarandus*) population. Even so, we did not find any caribou remains in bear scats. However, our results show that forestry practices, such as clearcutting near the caribou range, could contribute to increased bear presence and thus increase the probability of predation.

Keywords: black bear, habitat modification, habitat selection, low productive environment, phenology, resource selection function.

Résumé : Des hivers longs et neigeux combinés à une saison de croissance courte font en sorte que les forêts boréales sont un environnement improductif représentant un défi pour les ours noirs (*Ursus americanus*). Nous avons utilisé des fonctions de sélection des ressources (basées sur la télémétrie GPS de 16 ours), l'analyse de la diète, des relevés de la phénologie des plantes et des inventaires de végétation pour étudier les adaptations des ours noirs à la forêt boréale. Parce que les plantes sont grandement préférées dans les diètes des ours, nous nous attendions à ce que la composition du régime alimentaire reflète leur disponibilité temporelle. Nous prévoyions que les ours sélectionneraient des types de couvert forestier et des conditions topographiques spécifiques pour favoriser les plantes qui rempliraient leurs demandes énergétiques durant la période active. Nous avons aussi prédit que les ours sélectionneraient des habitats modifiés par les épidémies d'insectes ou la coupe forestière parce que ces perturbations augmentent probablement la disponibilité des ressources. Nous avons trouvé des évidences soutenant toutes nos prédictions. (1) La diète des ours était étroitement liée à la disponibilité des plantes. (2) Les ours ont fait des mouvements altitudinaux saisonniers et ont sélectionné des sites en fonction de la radiation solaire, suivant à la trace la disponibilité des plantes les plus digestibles. Ainsi, les ours dépendaient des graminées d'altitude au printemps, d'une variété de fruits charnus en été et principalement des baies de *Sorbus americana* en automne. (3) L'ouverture du couvert forestier résultant de coupes totales et d'épidémies d'insectes augmentait la disponibilité des ressources pour les ours et ces milieux ont été préférés de l'été à l'automne. Dans notre secteur d'étude, on considère les ours noirs comme des prédateurs d'une population de caribou (*Rangifer tarandus*) menacée, mais nous n'avons trouvé aucun reste de caribou dans les fèces des ours. Cependant, nos résultats démontrent que les pratiques de sylviculture comme la coupe totale près de l'habitat du caribou pourraient contribuer à augmenter la présence des ours et ainsi la probabilité de prédation.

Mots-clés : environnement peu productif, fonction de sélection des ressources, modification de l'habitat, ours noir, phénologie, sélection de l'habitat.

Nomenclature: Wilson & Reeder, 1993; Marie-Victorin, 1995.

Introduction

Environmental productivity is considered to be a major factor acting on ecosystem dynamics (Oksanen & Oksanen,

2000; Loreau *et al.*, 2001). Productivity generally decreases along a latitudinal gradient from the equator to the poles (Hawkins *et al.*, 2003). In North America, the productivity of hardwood and mixed forests, which are found mainly in central USA, contrasts with that of the boreal forest in Canada and Alaska (Crête, 1999). The boreal forest biome is severely limited by unique biophysical constraints and

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displays low levels of taxonomic diversity and productivity (Hobbie, Jensen & Chapin, 1994; Pastor *et al.*, 1996). Increasing resource extraction in this biome, such as by forestry practices, poses the risk of extinction of local species (Pastor, Light & Sovell, 1998).

Forest exploitation is considered to have many negative impacts. Habitat loss and fragmentation are often associated with forest exploitation (Spies, Riple & Bradshaw, 1994; Lofman & Kouki, 2003; Etheridge *et al.*, 2006) and thus directly influence the carrying capacity for many animal populations (Haila, 1999; Schmiegelow & Monkkonen, 2002). Development of forestry road networks is also considered to have negative consequences through habitat loss and modification (Forman & Alexander, 1998; Ortega & Capen, 1999) and increased human disturbance (Dyer *et al.*, 2001; Nellemann *et al.*, 2001). Forestry activities can also be beneficial for some vertebrate species, however. Regenerated sites following timber harvest can often be characterized by higher plant diversity than unharvested forests (Peltzer *et al.*, 2000). Plant regeneration has been shown to provide food and cover for several mammals (Etcheverry, Ouellet & Crete, 2005; Potvin, Breton & Courtois, 2005). Finally, forest roads that increase access could be used as travel corridors (Bennett, 1991; Noss, 2001) or provide conditions that improve predator efficiency (Bergerud, 1981; James & Stuart-Smith, 2000).

Boreal forest comprises the largest continuous habitat occupied by black bear (Young & Ruff, 1982). However, few studies have described bear habitat selection in this biome, and most were conducted in western Canada and the USA (Jonkel & Cowan, 1971; Young & Ruff, 1982; Schwartz & Franzmann, 1991). Moreover, none have dealt with the potential impact of forest exploitation on the presence of this opportunistic predator near the population of an endangered species. Black bears are known to be one of the most versatile species of mammals and are widely distributed in North America, from Labrador (Canada) to Florida (USA) and from Alaska (USA) to northern Mexico (Powell, Zimmerman & Seaman, 1997), but boreal forest could provide particularly challenging conditions for this species. Conifer tree stands do not provide the fatty mast used by black bears in southern latitudes to gain weight before denning (Lindzey & Meslow, 1976; Rogers, 1987). Moreover, diversity and productivity of soft mast-producing species tend to be lower in coniferous than deciduous forests (Jonkel & Cowan, 1971; Clark *et al.*, 1994). Northern black bears could compensate for a low-protein diet by preying on ungulate calves, such as moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and caribou (*Rangifer tarandus*) (Mathews & Porter, 1988; Schwartz & Franzmann, 1991; Linnell, Aanes & Andersen, 1995). This predation could have an important impact on the dynamics of boreal ungulate populations (Ballard, 1992; Messier, 1994; Rettie & Messier, 1998). Black bears are considered one of the main predator species of the endangered Gaspé caribou (Crête & Desrosiers, 1995), and habitat modification through human activities could potentially exacerbate predation pressure on this population.

We used resource selection functions, diet analysis, plant phenology surveys, and vegetation inventories to study

adaptations of black bears to low productivity in the boreal forest. Due to the large proportion of herbivory in black bear diets (Welch *et al.*, 1997), we anticipated that bears would make choices among land cover types and topographic conditions in order to track temporal and spatial availability of fruiting plants throughout the active season. We also expected the composition of bear diet to reflect temporal availability of food resources. Finally, because boreal forest represents a poor-quality habitat for black bears, we suspected that habitat modification from natural or anthropic origins, such as insect outbreaks or forest logging, would benefit black bear populations by increasing resource availability and should be selected by bears (Mitchell & Powell, 2003). Potential implications of our results for conservation of the endangered Gaspé caribou population are discussed.

Methods

STUDY AREA

The study area, defined as the area used by all radio-collared bears (100% minimum convex polygon, MCP), covers approximately 3400 km², including a large part of the Gaspésie Conservation Park (802 km², 48° 46' N, 65° 30' W; Québec, Canada). This mountainous region comprises the McGerrigle Mountains, dominated by Mt. Jacques Cartier (1268 m), and the Chic Chocs Mountains, including Mt. Albert (1154 m) and Mt. Logan (1128 m). Alpine tundra vegetation found on summits above 1000 m consisted of krumholtz, Ericaceae, and a carpet of lichens, mosses, and graminoids (Sirois & Grantner, 1992). The subalpine zone (900–1000 m) was characterized by an open coniferous forest, with trees becoming stunted with increasing altitude. The foothill zone (100–900 m) was boreal forest composed of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), black spruce (*P. mariana*), yellow birch (*Betula alleghaniensis*), and white birch (*B. papyrifera*) (Boudreau, 1981). Most areas situated immediately outside the park were subject to forestry exploitation, and 25% of these areas have been cut in the last 20 y. The region included an endangered population of mountain caribou (*Rangifer tarandus* caribou) located mainly within the boundaries of the Gaspésie Conservation Park. Black bears are considered to be one of the main predators of caribou calves in this population (Crête & Desrosiers, 1995).

BLACK BEAR DATA

Black bears were captured within a 5-km radius to the south and east of Mt. Logan during July in 2002, 2003, and 2004. Three types of leghold snares were used, all with padded cables and coil springs to minimize injury (Lemieux & Czetwertynski, 2006). Captured bears were anaesthetized with a dart containing a mixture of tiletamine and zolazepam (Telazol®) at a dosage of 5 mg·kg⁻¹ that was fired from a CO₂-powered pistol (Palmer Cap-Chur Inc., Powder Springs, Georgia, USA). Twenty-four black bears (15 males and 9 females) were equipped with global positioning system (GPS) radiocollars (GPS 3000, GPS 3300, and GPS 2200, LOTEK Engineering Inc., Newmarket, Ontario, Canada) and followed from July 2002 to November 2004. Collars were programmed to take one location every hour or every 4 h, depending on the model capacity. We recovered

the radiocollars in winters 2003, 2004, and 2005 by visiting hibernation dens. Bears were then anaesthetized using a CO₂-powered pistol or a “Jab-stick”, and some radiocollars were replaced by collars with fresh batteries. Because of collar failures, we used data from 16 different bears, of which 4 were followed for 2 y. Handling procedures were approved by the Animal Care Committees of the Ministère des Ressources Naturelles et de la Faune (CPA-Faune 02-00-01, 02-00-02, 03-00-02, and 04-00-16) and the Université du Québec à Rimouski (CPA-13-02-02).

HABITAT USE AND SEASONALITY

Black bears are well known to adapt to seasonal changes in food availability (Rogers, 1987; Powell, Zimmerman & Seaman, 1997). Because this adaptability is linked to changes in habitat use throughout the year (Garshelis & Pelton, 1981; Powell & Seaman, 1990; Samson & Huot, 1998), we used 2 complementary approaches to determine the timing of these habitat and diet preferences.

First, taking into account the ecology of black bears and limitations in the use of forest maps (Dussault *et al.*, 2001), we grouped data from digitized ecoforest maps (1:20 000) from the Ministère des Ressources Naturelles du Québec into 10 land cover types based on tree stand composition, age, and structure (see Table I for a list). We documented plant phenology during 2003 and 2004 using 4 randomly distributed 1-m² plots in each of the different land cover types present in our study area. Each plot ($n = 40$) was visited every 2 weeks from June to October. We noted developmental stages of each plant species (dormancy, foliage, flowering, immature fruits, mature fruits) and paid particular attention to the date of appearance and disappearance of fruits. We then defined phenology using the mean number of species in each of the 5 developmental stages at each evaluation date. We tested the effect of year on phenology using an analysis of variance (ANOVA) with repeated measures (PROC MIXED with repeated statement; SAS Institute, 2004).

Second, in order to evaluate whether changes in plant phenology were reflected in bear diet, scats were collected

on 3 predetermined 30-km forest road networks, covering most of the study area. After an initial removal of all visible scats, we surveyed this network every 2 weeks from 1 June to 30 September, 2003 and 2004. In addition, opportunistic sampling was carried out during other field activities (45% of collected scats). Only fresh scats (greasy, smelly, or containing fresh fruit parts) were collected and analyzed. Estimated deposition dates (based on appearance of other scats with known deposition date) were used to follow diet composition throughout the year. Scat contents were analyzed using a point-sampling method derived from Chamrad and Box (1964), with the number of sampling points fixed at 50 items per scat (Boileau, Crête & Huot, 1994). We identified items using dissecting microscopes (6 to 40×), identification guides and a reference collection. We double-checked mammal hairs using a microscope (40 to 1000×), hair guides (Adorjan & Kolenosky, 1980), and comparison with hairs in our reference collection.

RESOURCE SELECTION FUNCTIONS

We used resource selection functions (RSFs; Manly *et al.*, 2002) to analyze habitat selection by black bears at the home-range scale (third order of selection; Johnson, 1980). We delineated individual home ranges using 100% minimum convex polygons (MCPs; Mohr, 1947). Recent literature criticizes the use of this method (Laver & Kelly, 2008). However, this method is adequate to delineate the area that could potentially be visited by a bear. We did not use kernel estimates because this method already implies a selection process as it takes into account the intensity of use (*i.e.*, density of locations) to estimate the home range. The area delineated by kernel thus reduces the potential contrast between conditions available and conditions used. Resource use estimated by GPS locations was compared with resource availability obtained from random locations (2000 points/home range), using logistic regressions (Boyce & McDonald, 1999; Manly *et al.*, 2002). Analyses were separated into 3 time periods based on major shifts in bear diet. For each period, we only used individuals with a data set covering > 80% of the time interval considered. Sample

TABLE I. Mean (SE) lateral cover, vertical cover, deciduous and coniferous tree basal area, deciduous and coniferous sapling density, and mass of fruits present in different land cover types within the study area of the Gaspé Peninsula, southeastern Québec, Canada. Differences between land cover types were tested using ANOVA followed by Tukey *post hoc* tests. When application conditions for ANOVA were not met (*i.e.*, for deciduous basal area and deciduous and coniferous sapling densities), we used a Kruskal–Wallis test followed by Dunn *post hoc* tests. For each vegetation characteristic, values having different letters within a column indicate a significant difference between land cover types ($P < 0.05$).

Land cover type	Lateral cover (%)	Vertical cover (%)	Basal area		Sapling density		Fruit mass (g·m ⁻²)
			Deciduous (m ² ·ha ⁻¹)	Coniferous (m ² ·ha ⁻¹)	Deciduous (no.·ha ⁻¹)	Coniferous (no.·ha ⁻¹)	
Barren	87.1 (5.1) ^a	20.8 (4.7) ^{c,d}	0.0 (0.0) ^c	8.6 (3.0) ^{b,c,d}	0 (0) ^b	688 (254) ^a	0.9 (0.4) ^d
Deciduous	86.1 (3.5) ^a	94.9 (1.9) ^a	11.1 (1.3) ^a	6.8 (1.7) ^{c,d,e}	2401 (389) ^a	790 (309) ^a	3.1 (0.6) ^{c,d}
Mixed with coniferous dominance	90.7 (2.5) ^a	80.0 (4.0) ^b	7.2 (1.3) ^{a,b}	12.7 (1.9) ^{b,c}	3938 (1117) ^a	1344 (487) ^a	4.2 (1.1) ^{b,c,d}
Coniferous 20-50 y	85.4 (3.5) ^{a,b}	68.1 (7.9) ^b	0.9 (0.6) ^c	26.9 (3.7) ^a	208 (147) ^{a,b}	903 (391) ^a	4.0 (1.8) ^{a,b,c,d}
Closed mature coniferous	80.8 (5.0) ^{a,b}	70.8 (5.4) ^b	0.8 (0.8) ^c	27.8 (3.0) ^a	1125 (550) ^{a,b}	1438 (672) ^a	4.5 (1.3) ^{a,b,c,d}
Open mature coniferous	87.2 (3.9) ^a	35.2 (5.0) ^c	0.2 (0.2) ^c	18.6 (3.1) ^{a,b}	0 (0) ^b	500 (156) ^a	0.7 (0.7) ^d
Natural disturbance	88.5 (4.1) ^a	77.7 (4.0) ^b	2.4 (0.9) ^{b,c}	12.6 (2.4) ^{b,c}	4137 (1079) ^a	1310 (464) ^a	7.8 (1.1) ^{a,b}
Partial cut	81.2 (5.5) ^{a,b}	72.3 (8.4) ^b	2.2 (1.1) ^{b,c}	24.7 (3.7) ^a	284 (176) ^a	1818 (902) ^a	3.8 (1.1) ^{b,c,d}
Clearcut 0-5 y	58.3 (8.0) ^b	5.5 (2.0) ^{d,e}	0.4 (0.3) ^c	0.0 (0.0) ^e	188 (95) ^{a,b}	563 (218) ^a	7.4 (1.0) ^{a,b,c,f}
Clearcut 5-20 y	76.0 (3.7) ^{a,b}	4.3 (3.0) ^e	0.4 (0.4) ^c	0.2 (0.2) ^{d,e}	563 (329) ^{a,b}	1750 (690) ^a	9.7 (1.1) ^a

† This value was likely overestimated because fruit mass was based on plant cover, and in most cases fruit production does not actually begin until the fourth year after logging.

sizes were 11, 16, and 9 individuals with 754 ± 180 , 283 ± 58 , and 606 ± 105 locations·bear⁻¹ for spring, summer, and autumn, respectively. Estimates from logistic regression were used in RSF models with the following form:

$$w(x) = \exp(\beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n) \quad [1]$$

where $w(x)$ was the RSF and β_i was the estimate for the variable x_i (Manly *et al.*, 2002).

We applied both conditional fixed-effect and mixed-effect logistic models to fit our data. These 2 methods avoided pseudo-replication by taking the individual, and not the telemetry location, as the unit of measure (Otis & White, 1999). In conditional fixed-effect regressions, all locations for each individual were considered as an independent stratum (Strata statement in PROC PHREG; SAS v9.1.3; SAS Institute, 2002). Standard errors and associated significance levels were then estimated using a robust sandwich estimate of the covariance matrix (Lin & Wei, 1989). In mixed-effect regressions, the individual was considered a random variable in PROC NLMIXED (SAS v9.1.3; SAS Institute, 2002). Effect of sex on habitat selection was tested only in NLMIXED, because this test was not possible within the conditional fixed-effect regression (individual was considered as one stratum and there exists only one sex per individual). Comparisons between resulting RSF models were made using Akaike's Information Criterion (AIC; Burnham & Anderson, 2002). One model per sex was run when an effect was detected for a given season. We did not explore year-to-year variation in habitat selection because sample sizes precluded yearly stratification of data. Finally, model fit was evaluated using all data as test data in the adapted version of K-Fold cross-validation (Boyce *et al.*, 2002) proposed by Johnson *et al.* (2006).

Contrary to the results of Gillies *et al.* (2006), models based on mixed effects had a poorer fit (lower R^2 for linear regression test, significant chi-square goodness-of-fit test, slope and intercept of the linear regression significantly different from 1 and 0, respectively; Johnson *et al.*, 2006) than those based on conditional fixed effects. Thus, we only present results obtained from the second method.

RSF VARIABLES

Based on previous literature, we analyzed whether habitat selection by black bears varies according to topography (Garshelis & Pelton, 1981; Unsworth, Beecham & Irby, 1989), presence of water bodies and roads (Unsworth, Beecham & Irby, 1989; Gaines *et al.*, 2005), or land cover type (Samson & Huot, 1998; Mitchell & Powell, 2003). For each GPS location and random point, we measured 4 topographic covariates (elevation, slope position, inclination, and solar irradiance) using ArcGIS v9.0 (ESRI, 2004). Similarly, we measured the minimum distance of each point to a road or water body and used the ecoforest maps to classify each point into one of 10 land cover types. Because altitude could influence both spatial and temporal availability of black bear resources (Garshelis & Pelton, 1981), we also fitted the square of the altitude into the models to test for non-linear relationships. Topographic and distance variables were calculated for each cell of 10-m resolution maps covering the study area. Elevation

and slope maps were generated from a triangulated irregular network (TIN) surface model constructed from a 1:20 000 topographic map (MRNQ, 1992) using ArcGIS v9.0 (ESRI, 2004). Slope position (upper, middle, lower, flat) was obtained using the "topographic position index" extension (Jenness, 2005) for ArcView v3.2a (ESRI, 2000) and landscape elevation within a 250-m radius around each cell of the raster. Solar radiation received on Julian day 172 (spring solstice) was calculated using scripts developed by Kumar, Skidmore, and Knowles (1997) under ArcInfo v9.0 (ESRI, 2004). Distances from road and water were calculated from digital maps. Finally, land cover maps (see above) were generated for 2002 and updated for 2003 and 2004 to incorporate changes (*e.g.*, through logging) between years.

LAND COVER CHARACTERISTICS

We described characteristics of the 10 land cover types through field sampling carried out in 2003. Because of logistic constraints, 10 sites for each land cover type were randomly chosen from the entire study area using a geographic information system (ArcGIS v9.0; ESRI, 2004). Cover provided by habitat was estimated as lateral cover or the percentage of visual obstruction on a 150 × 30-cm profile board placed 15 m from the centre of the sample site (Nudds, 1977). Vertical cover was also evaluated by counting the number of points that were under cover along a 15-m transect by sampling every 1.5 m from the centre of the sample site (adapted from Potvin, Bélanger & Lowell, 1999). Lateral and vertical covers were estimated in the 4 cardinal directions. Since habitat selection could be linked not only to structure, but also to composition of the habitat, we measured basal area of coniferous and deciduous trees (diameter at breast height [DBH] ≥ 10 cm) using a factor-2 prism (Grosenbaugh, 1952). Density of coniferous and deciduous saplings (DBH < 10 cm) was measured by counting the number of each sapling type in a 16-m² plot centred on the sample site. Because fruits usually represent a large proportion of bear diet (Welch *et al.*, 1997; Rode & Robbins, 2000), we measured cover of shrub species in the 16-m² plot and cover of herbaceous species in four 1-m² plots adjacent to but outside the corners of the 16-m² plot. In order to extrapolate fruit biomass available in each land cover type, we placed additional 1-m² plots in randomly located patches of herbaceous plants (10 plots sampled per species). We estimated percent cover of the species considered and collected all mature fruit biomass. For shrubs, we measured 10 specimens per species (length, width, and height) and collected all fruits. Fruits were then dried and weighed. Finally, we estimated linear relationships between percent cover and fruit biomass for each plant species and calculated fruit biomass for each land cover type (see above). Differences between land cover types were tested using ANOVA followed by Tukey *post hoc* tests. If assumptions for ANOVA were not met, we used Kruskal–Wallis tests followed by Dunn *post hoc* tests.

Results

PHENOLOGY AND DIET ANALYSIS

Plant phenology (Figure 1) was similar between 2003 and 2004 ($F = 1.1$, $df = 1$, $P = 0.324$). Because the 2003

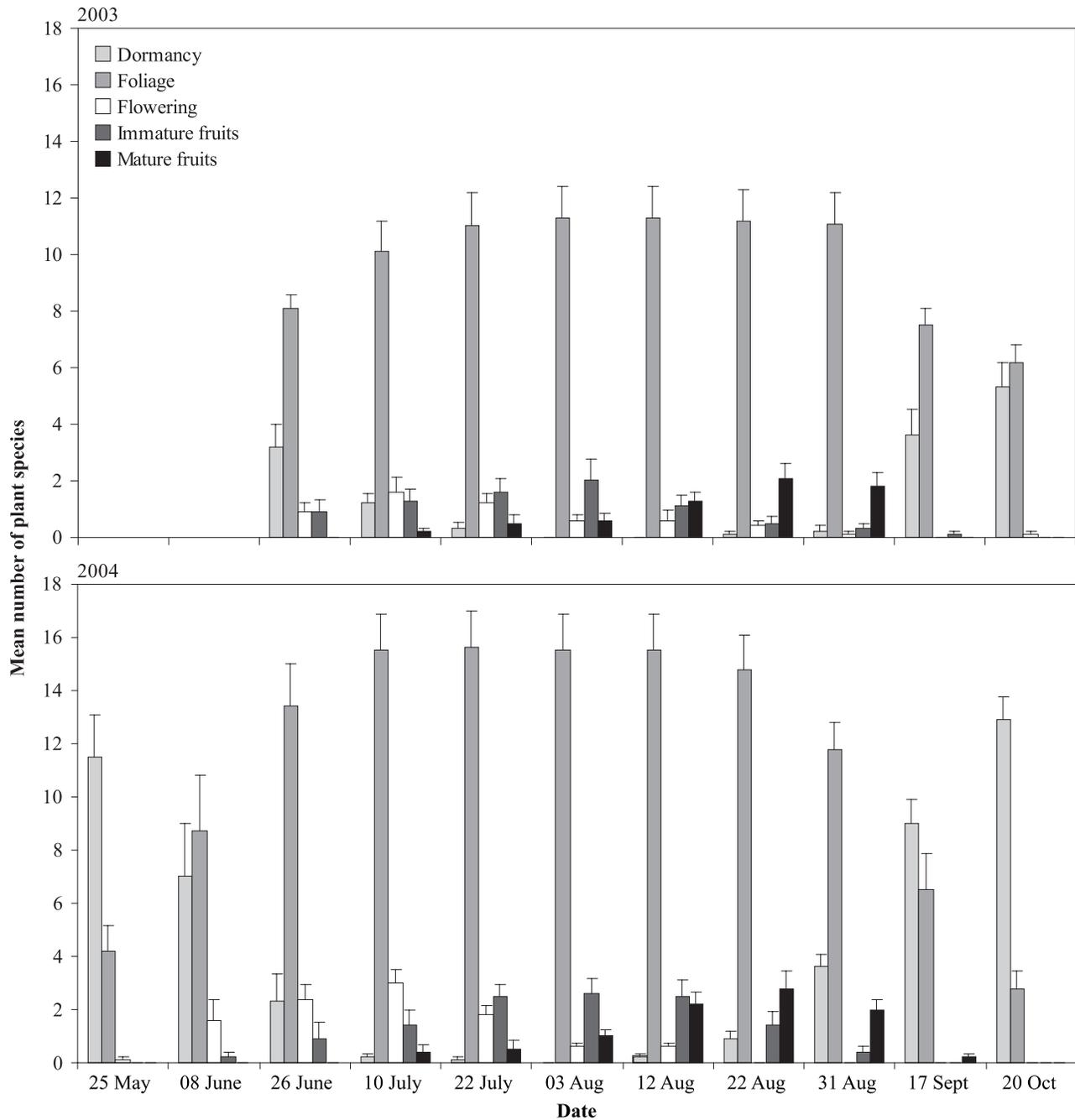


FIGURE 1. Plant phenology as mean number of plant species (+ SE) in 5 different developmental stages observed every 2 weeks across 10 different land cover types in 2003 and 2004 in the Gaspé Peninsula, southeastern Québec, Canada. Note: the 2003 survey only began at the end of June.

survey began only at the end of June, flowering and first immature fruit appearance dates could not be assessed that year. Most species, however, flowered and produced immature fruit on the same dates in both years, *i.e.*, around 10 July and the first week of August, respectively. The first mature fruits appeared on 10 July, with the greatest number of species having mature fruits on 22 August. Fruits disappeared in the first week of September.

Scat analysis ($n = 96$) revealed 3 distinct periods of black bear diet (Figure 2). (1) During spring (den emergence to mid-July), graminoids represented the greatest

proportion (70%) of the diet. Moose calves represented the second most important item but comprised only 5% of the diet in spring. (2) Summer (mid-July to end of August) was characterized by the appearance of a wide diversity of fruits in the diet, including red-osier dogwood (*Cornus stolonifera*), wild Sarsaparilla (*Aralia nudicaulis*), mountain holly (*Nemopantus* sp.), raspberries (*Rubus* sp.), elderberries (*Sambucus nigra*), and strawberries (*Fragaria* sp.). Graminoids still composed 17% of bears' diet. (3) In autumn (1 September to den entry), bears consumed mainly berries of mountain ash (*Sorbus americana*), which

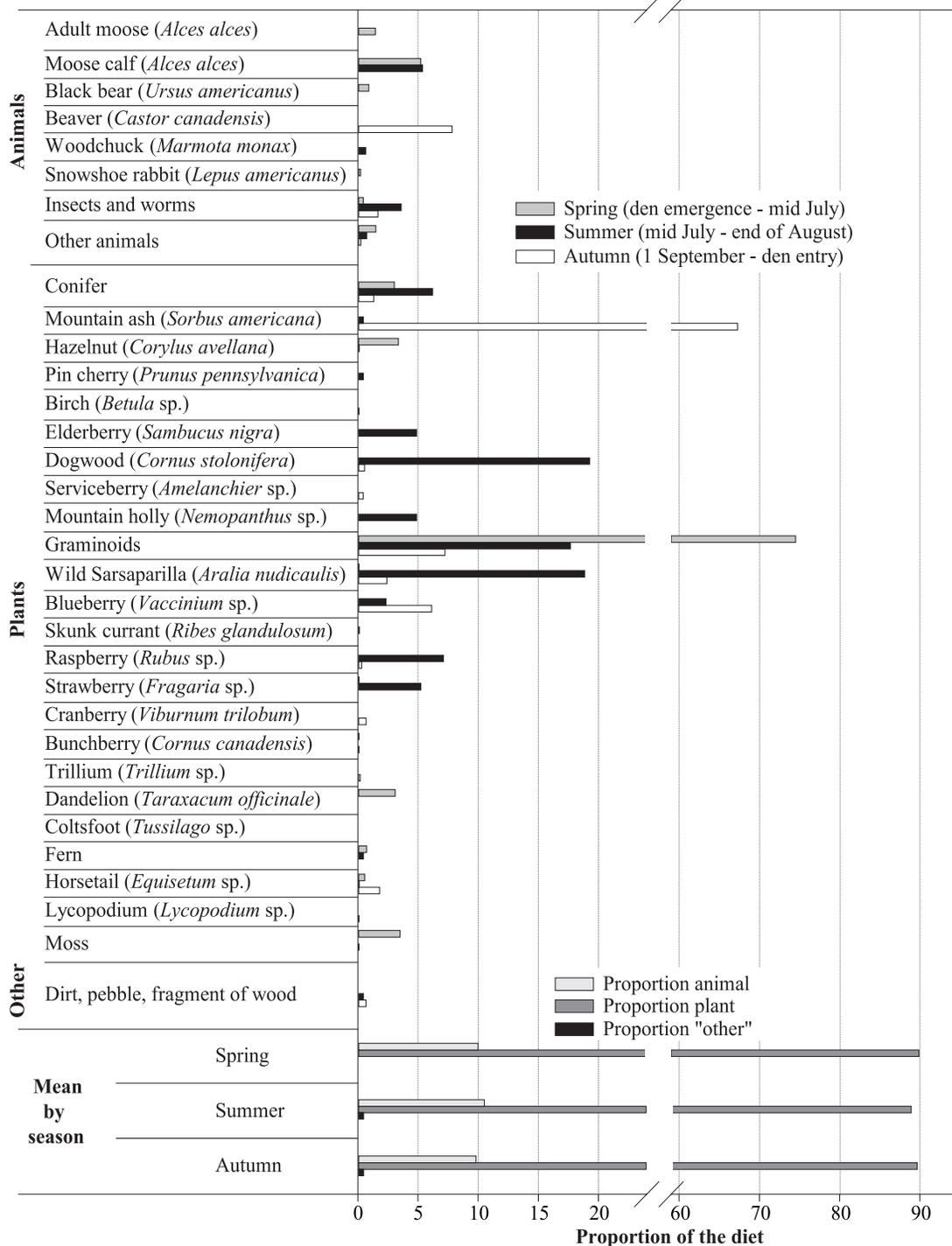


FIGURE 2. Items consumed by black bears during spring (den emergence to mid-July), summer (mid-July to end of August), and autumn (1 September to den entry) based on scat samples ($n = 96$; point sampling method) collected during 2003 and 2004 in the Gaspé Peninsula, southeastern Québec, Canada. "Other animals" refers to hairs ingested during grooming, micro-mammal hairs, eggs and unidentified bone fragments. "Insects and worms" comprised wasps, ants, worms, and unidentified insects.

represented over 65% of the diet. Blueberries (*Vaccinium* sp.) and graminoids were also consumed in this season. Beaver constituted approximately 8% of the autumn diet and probably originated from baiting carried out by trappers. Black bear diet was dominated by plants (approximately 90%) in all 3 periods. No trace of caribou was found.

LAND COVER CHARACTERISTICS

Except in 0- to 5-y-old clearcuts, lateral cover exceeded 75% in all land cover types (Table I). Differences were more pronounced for vertical cover. Land cover generated from clearcuts < 20 y were characterized by a lower vertical cover (< 6%) than other land cover types. These were

also land cover types that had high estimated fruit mass per unit area. Not surprisingly, barren and open mature coniferous land cover, mostly located at high altitude with stressful conditions for plant development, were open habitats (vertical cover of 21 and 35%, respectively) with the lowest fruit mass. As expected, closed mature and 20- to 50-y-old coniferous land cover had the highest coniferous basal area. As confirmed by tree basal area, land covers that originated from natural disturbance were primarily coniferous stands. Natural disturbance land covers contained numerous deciduous saplings and provided the second largest fruit mass per unit area. Partial cuts, which were all performed in coniferous stands in our study area, were very similar in almost all characteristics to the coniferous 20–50 y land cover.

RSFs

Comparison of RSF models (Table II) showed that global models comprising topographic, distance, and land cover variables fit the data better than models comprising only one or a combination of 2 groups of variables. Complementary analyses also showed that combinations of single variables did not improve models.

Seasonal models allowed us to detect variations in habitat selection over the course of the year. No sex effect was detected in spring and regression suggested that the RSF model provided a good fit to the data ($R^2 = 0.907$; Table III), as did the chi-square goodness-of-fit test ($P = 0.855$). Results for spring indicated that bears occupied

TABLE II. Comparison of models used to predict relative occurrence of black bears in the study area during spring, summer (1 model per sex), and autumn. Models were ranked based on Akaike’s Information Criterion (AIC) values. Delta AIC (Δ_i) measures the difference between each model and the best model (AICs for best models are 130 855.7; 18 287.5; 49 945.3, and 75 705.3 for spring, summer male, summer female, and autumn, respectively). Akaike weights (w_i) indicate the probability that a model is best among the entire set of candidate models. K_i is the number of parameters used in each model.

Season	Sex	Model	K_i	Δ_i	w_i
Spring	Both	Global (Topo + Dist + Cover)	18	0.0	1.000
		Topo + Cover	16	176.1	< 0.001
		Dist + Cover	11	554.0	< 0.001
		Cover	9	717.8	< 0.001
		Topo + Dist	9	875.1	< 0.001
		Topo	7	983.5	< 0.001
		Dist	2	1835.8	< 0.001
Summer	Male	Global (Cover + Topo + Dist)	18	0.0	1.000
		Topo + Cover	16	86.7	< 0.001
		Dist + Cover	11	160.6	< 0.001
		Cover	9	233.4	< 0.001
		Topo + Dist	9	244.1	< 0.001
		Topo	7	400.6	< 0.001
		Dist	2	572.2	< 0.001
Summer	Female	Global (Cover + Topo + Dist)	18	0.0	0.992
		Topo + Cover	16	9.8	0.008
		Dist + Cover	11	202.3	< 0.001
		Cover	9	208.7	< 0.001
		Topo + Dist	9	404.6	< 0.001
		Topo	7	457.4	< 0.001
		Dist	2	1079.5	< 0.001
Autumn	Both	Global (Cover + Topo + Dist)	18	0.0	1.000
		Topo + Cover	16	139.0	< 0.001
		Topo + Dist	9	265.0	< 0.001
		Topo	7	407.4	< 0.001
		Dist + Cover	10	461.3	< 0.001
		Cover	9	793.5	< 0.001
		Dist	2	885.4	< 0.001

Note: “Topo” included seven topographic variables (elevation, elevation², slope, 4 classes of slope position, solar radiation), “Dist” included 2 distance variables (distance to a water body and a road) and “Cover” included 10 classes of land cover types (see Table 1). For categorical variables (slope position and land cover type), one of the class is considered as a reference (“flat slope” and “mixed with coniferous dominance”, respectively) and was thus not considered in the number of parameters.

TABLE III. Fit of seasonal resource selection functions of black bears through linear regressions, goodness-of-fit tests, and Spearman rank correlations for expected versus observed frequencies in 10 bins of RSF values (Johnson *et al.*, 2006).

Season	Sex	Linear regression			Goodness-of-fit test			Rank correlation	
		Intercept	Slope	Adjusted R^2	χ^2	df	P -value	r_s	P -value
Spring	Both	0.003	0.967	0.907	4.75	9	0.855	1.000	< 0.001
Summer	Male	0.001	0.903	0.965	13.56	9	0.139	0.903	< 0.001
	Female	0.058	0.419 ^b	0.132	84.15	9	< 0.0001	–0.321	0.365
Autumn	Both	0.040 ^a	0.596 ^c	0.951	7.83	9	0.552	0.988	< 0.001

^a Intercept significantly different from 0.
^b Slope not significantly different from 0.
^c Slope significantly different from 1.

sites found at moderate to high altitudes (Figure 3; Table IV) and selected steep, upper slopes in areas where solar irradiation was high (Table IV). Bears also preferred road proximity. Barren and natural disturbance were the land cover types most selected, followed by mature coniferous (both closed and open). Deciduous and clearcut 0–5 y land covers were avoided.

In summer, habitat selection differed between sexes ($t = 3.47$, $df = 12$, $P < 0.005$). Regression and the chi-square goodness-of-fit test indicated that the summer RSF

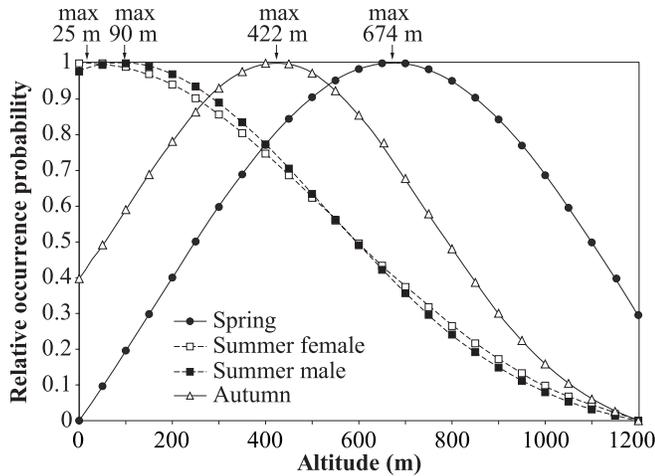


FIGURE 3. Relationship between the relative probability of occurrence of black bears and altitude. Coefficients were from the resource selection functions (RSFs) derived from radio-collared bears followed across 3 seasons from July 2002 to November 2004 in the Gaspé Peninsula, southeastern Quebec, Canada (see Table II for RSF models).

model for males fit the data well ($R^2 = 0.965$ and $P = 0.139$, respectively; Table III). Males were located at low altitudes (Figure 3) and sought gentle, upper slopes (Table IV). Male bears also tended to favour water proximity ($p = 0.057$), but stayed further away than expected from roads (Table IV). Barren, natural disturbance, and clearcut 5–20 y land covers were selected. Clearcut 0–5 y and partial cut land covers were avoided as well as deciduous, coniferous 20–50 y, and mature coniferous habitats.

The summer RSF model for females fit the data poorly ($R^2 = 0.132$ and $P < 0.001$ for regression and chi-square test, respectively; Table III), suggesting that female strategies differed between individuals. The model, however, indicated that females used sites found at low altitudes (Figure 3), selecting steep, upper slopes where solar irradiation was strong (Table IV). Females generally avoided roads but made no selection with respect to distance to water. Barren, natural disturbance and clearcut land covers were selected, whereas partial cut, deciduous and all coniferous stands were avoided (Table IV).

No sex effect was detected for habitat selection in autumn. Regression and the chi-square goodness-of-fit test ($R^2 = 0.951$ and $P = 0.552$) showed that the autumn RSF model was a good overall fit to the data. However, the regression also showed that the RSF overestimated values since the slope was significantly different from 1 (slope = 0.596; $P < 0.001$; Table III). Removing the last bin of data (*i.e.*, higher RSF values) from the calculation led to a regression with a robust fit (adjusted $R^2 = 0.944$) that was characterized by a slope that did not differ from 1 ($P = 0.085$), suggesting that only a small fraction (10% of the study area) was overestimated. In autumn, bears occupied

TABLE IV. Estimated coefficients (\pm SE) of seasonal RSF models for black bears followed between July 2002 and November 2004 in the Gaspé Peninsula, southeastern Quebec, Canada. Because of a significant sex effect, 1 model per sex is presented for summer. Standard errors were obtained using the robust sandwich estimator (Lin & Wei, 1989). Significant values ($P < 0.05$) are highlighted in bold (+) or grey (–). For continuous variables, the hazard ratio indicates the proportional increase (> 1) or decrease (< 1) in the probability of occurrence of bears for an increase of 1 unit (*e.g.*, for each degree of increase in slope). For categorical variables, the hazard ratio indicates whether a category was more likely (> 1) or less likely (< 1) to be used relative to a reference category. The reference category was “flat slope” for slope position and “mixed with coniferous dominance” for land cover type.

		Season							
		Spring ($n = 11$)		Summer male ($n = 8$)		Summer female ($n = 8$)		Autumn ($n = 9$)	
		Estimates (\pm SE)	Hazard ratio	Estimates (\pm SE)	Hazard ratio	Estimates (\pm SE)	Hazard ratio	Estimates (\pm SE)	Hazard ratio
Topography	Elevation (km)	2.539 (\pm 0.498)	12.665	0.483 (\pm 0.767)	1.620	0.099 (\pm 0.432)	1.104	3.987 (\pm 0.752)	53.874
	Elevation ²	–1.882 (\pm 0.408)	0.152	–2.603 (\pm 0.777)	0.074	–1.919 (\pm 0.405)	0.147	–4.723 (\pm 0.684)	0.009
	Slope (degree)	0.027 (\pm 0.002)	1.027	–0.021 (\pm 0.004)	0.979	0.014 (\pm 0.002)	1.014	0.005 (\pm 0.002)	1.005
	Upper slope	0.061 (\pm 0.056)	1.063	0.373 (\pm 0.097)	1.452	0.291 (\pm 0.063)	1.338	0.364 (\pm 0.091)	1.439
	Middle slope	–0.280 (\pm 0.054)	0.756	0.235 (\pm 0.092)	1.265	0.173 (\pm 0.057)	1.189	0.578 (\pm 0.078)	1.782
	Lower slope	–0.328 (\pm 0.061)	0.720	0.120 (\pm 0.104)	1.128	0.126 (\pm 0.063)	1.134	0.515 (\pm 0.085)	1.674
	Radiation (kWh·m ^{–2})	0.332 (\pm 0.036)	1.394	0.120 (\pm 0.076)	1.128	0.243 (\pm 0.038)	1.275	–0.147 (\pm 0.030)	0.864
Distances	To water (km)	–0.162 (\pm 0.097)	0.850	–0.306 (\pm 0.161)	0.737	0.097 (\pm 0.095)	1.102	–0.522 (\pm 0.124)	0.593
	To road (km)	–0.406 (\pm 0.047)	0.666	0.464 (\pm 0.038)	1.591	0.152 (\pm 0.035)	1.164	0.312 (\pm 0.038)	1.366
Land cover type	Barren	0.670 (\pm 0.078)	1.953	0.378 (\pm 0.186)	1.459	0.384 (\pm 0.103)	1.468	–0.115 (\pm 0.086)	0.891
	Deciduous	–0.775 (\pm 0.151)	0.461	–0.335 (\pm 0.119)	0.715	–0.458 (\pm 0.097)	0.632	–0.336 (\pm 0.097)	0.714
	Coniferous 20–50 y	–0.066 (\pm 0.072)	0.936	–0.964 (\pm 0.121)	0.381	–0.363 (\pm 0.069)	0.696	–0.563 (\pm 0.088)	0.569
	Closed mature coniferous	0.425 (\pm 0.063)	1.530	–1.095 (\pm 0.142)	0.335	–0.137 (\pm 0.063)	0.872	0.007 (\pm 0.060)	1.007
	Open mature coniferous	0.371 (\pm 0.072)	1.449	–0.181 (\pm 0.154)	0.834	–0.584 (\pm 0.084)	0.558	–0.067 (\pm 0.102)	0.935
	Natural disturbance	0.716 (\pm 0.055)	2.047	0.296 (\pm 0.081)	1.344	0.570 (\pm 0.054)	1.768	–0.011 (\pm 0.062)	0.989
	Partial cut	–0.207 (\pm 0.140)	0.813	–0.505 (\pm 0.158)	0.603	–0.225 (\pm 0.094)	0.799	–0.147 (\pm 0.109)	0.863
	Clearcut 0–5 y	–0.379 (\pm 0.173)	0.685	–1.473 (\pm 0.382)	0.229	0.401 (\pm 0.100)	1.493	0.150 (\pm 0.135)	1.162
Clearcut 5–20 y	–0.189 (\pm 0.100)	0.828	0.341 (\pm 0.132)	1.407	0.275 (\pm 0.070)	1.317	0.624 (\pm 0.083)	1.866	

intermediate altitudes (~400 m; Figure 3) and selected steep slopes but the relationship was weak (see hazard ratio; Table IV). Sites selected by bears were more likely to be lower and middle sections of slopes than flat slope (67 and 78%, respectively; hazard ratios). Moreover, bears were located in sites with low solar irradiation and avoided roads but selected water proximity (Table IV). Clearcuts 5 to 20 y old were the only selected land cover type in autumn, whereas deciduous and coniferous 20–50 y land covers were avoided.

Discussion

Low productivity in the boreal forest represents a challenge to black bears. Long periods with snow cover (November to May in our study area) lead to a short growing season, which restricts the number of fruiting species and temporal availability of fruits. Moreover, biophysical constraints also induce the absence of the fatty mast-producing trees that are often used by black bears to gain weight before denning in autumn (Jonkel & Cowan, 1971; Lindzey & Meslow, 1976; Rogers, 1987). As a result, black bears in our study area were smaller (mean \pm SD of 94 ± 32 and 61 ± 16 kg for 19 adult males and 11 adult females, respectively; A. Mosnier, unpubl. data) than those of southern regions with richer habitats, such as New Hampshire, Pennsylvania, or North Carolina (120–183 kg and 83–92 kg for males and females, respectively; Smith, 1985). Black bear home ranges were very large (*ca.* 300 km² for males and 200 km² for females; Mosnier *et al.*, 2008), more than twice the size generally reported in other regions (Powell, Zimmerman & Seaman, 1997; Koehler & Piercea, 2003). Furthermore, low habitat productivity may explain the absence of territoriality in our study area (Mosnier *et al.*, 2008). In the mountainous Gaspé Peninsula, resource availability changed significantly at both seasonal and spatial scales. As we expected, black bears adapted to these conditions through seasonal adjustments in diet composition, habitat selection, and altitudinal movements. Unfortunately, these adaptations could increase encounter probability with members of the endangered Gaspé caribou population.

In accordance with many studies (Rogers, 1987; Boileau, Crête & Huot, 1994; Powell, Zimmerman & Seaman, 1997; Samson & Huot, 1998), our results showed that bear diet was closely linked to plant availability. The overall proportion of plants in the diet remained unchanged throughout the year, at around 90%. Specific composition of the diet, however, changed from very simple (mainly graminoids in spring and sorbs in autumn) to much more diverse when soft fruits became available in summer. Proportion of plants was high despite the relatively low plant diversity and scarcity of species preferred in southern regions (*e.g.*, buffalo berry [*Shepherdia* sp.], huckleberry [*Gaylussacia* sp.], and blueberry [*Vaccinium* sp.]). Also, moose density was very high in our study area (4 to 5 moose·km⁻², Lamoureux *et al.*, 2007). Bears thus likely had access to carcasses due to natural mortality or hunting accidents and are known to be effective predators of moose calves (Schwartz & Franzmann, 1991; Bertram & Vivion, 2002). Therefore, we expected to find a greater portion of ungulate meat in the diet. Moreover, unlike previous results,

only a very small proportion of the diet was composed of insects (Noyce, Kanno & Riggs, 1997). Rode, Robbins, and Shipley (2001) and Brown (1993) found that even when meat resources were abundant, plants comprised a very large fraction of grizzly bear seasonal diets. The large proportion of *Sorbus* sp. fruits in the autumn diet of black bears (67% in this study) was also found by Leblanc (2000) in the eastern part of the Gaspé Peninsula and seems to be an important alternative to hard mast. The clumped distribution of this resource permits bears to rapidly consume a large amount of fruit. As suggested for both the hibernating primate *Cheirogaleus medius* (Fietz & Ganzhorn, 1999) and bears (Rode & Robbins, 2000), excess energy from the consumption of a large quantity of fruit could be deposited as fat before hibernation in the absence of fatty mast.

Numerous studies have reported that black bears modify their habitat selection based on food availability (Garshelis & Pelton, 1981; Rogers, 1987; Powell, Zimmerman & Seaman, 1997; Davis *et al.*, 2006), but only some of them have taken plant phenology into account (Young & Beechman, 1986; Boileau, Crête & Huot, 1994; Costello & Sage, 1994; Davis *et al.*, 2006). Our field survey of phenology and simultaneous diet analysis led us to define time periods that were related to important shifts in habitat use. In an environment where food resources are particularly limited, habitat selection necessarily reflects a quest for the highest possible net energy gain. In our case, low productivity resulted in complex choices based on land cover types and topography. Thus, the use of upper portions of steep slopes located at high altitude during spring likely corresponded to sites with little winter snow accumulation. High solar irradiation in selected sites would result in areas where snow melts quickly and vegetation appears early. In most cases, the barren land cover type corresponded to that description. Albon and Langvatn (1992) suggested that the nutritive value of vegetation also increases with altitude. Bliss (1962), cited by Myrsetrud *et al.* (2001), noted a low presence of fibrous tissues in plants growing at high altitude. Considering the relatively low capacity of bears to digest fibre (Welch *et al.*, 1997), use of high-altitude sites may allow bears to find the most readily digestible source of forage available in that season.

Natural disturbances played an important role in bear habitat selection in spring as well as summer, as expected. Bears were found to use natural disturbances for resting over variable time periods, from one night to several days following initial den emergence (A. Mosnier, unpubl. data), likely benefiting from the high cover provided by numerous fallen trees (A. Mosnier, pers. observ.) in this land cover type (Table I) and possibly waiting for improved foraging conditions in spring while reducing energy expenditure. The use of natural disturbances during summer provided access to the second-highest availability of fruiting species in our study area (Table I).

Alteration of landscape by human activities, such as logging, creates openings in the forest canopy and increases availability of young stands with diverse regeneration (Costello & Sage, 1994; Samson & Huot, 1998; Mitchell & Powell, 2003). In our study, bears selected clearcuts 5–20 y old in summer and autumn. Openings in forest canopy

permitted growth of a large quantity of fruiting species, such as raspberries and dogwood (Greenberg, Levey & Loftis, 2007). Moreover, trees such as sorbs, the fruit of which composed a large part of the bear diet in autumn, could be more abundant several years after logging than in undisturbed stands (Newton *et al.*, 1989). In contrast, the use of clearcuts 0–5 y old was different between males and females. Females selected this land cover type in summer, whereas males clearly avoided it (Table IV). Selection of this habitat was surprising, because fruit availability was actually less than that estimated by plant cover (Table I). Although plant cover of fruiting species such as raspberries was extensive, production of fruit by colonizing species does not begin until the third or fourth year after logging (A. Mosnier, pers. observ.). A closer look at the data indicated that only 2 of the 8 females studied selected this land cover.

Roads, another source of landscape alteration, were also found to play a role in habitat selection by black bears. Our observation that bears selected sites close to roads during spring seems to contradict the findings of Gaines *et al.* (2005) that roads reduce habitat quality for black bears during all seasons. In our case, high-altitude roads were found mainly within the Gaspésie Conservation Park and had very limited traffic. Moreover, roadsides could offer large quantities of graminoid species (Watkins *et al.*, 2003), which we found in the spring diet (Figure 1). In summer and autumn, however, forestry roads located at low to intermediate altitudes were avoided even if associated with the land cover type (*i.e.*, older clearcuts) that tended to be selected by bears (see also Kasworm & Manley, 1990; Gaines *et al.*, 2005; Reynolds-Hogland & Mitchell, 2007).

Black bears may use higher altitudes in autumn than in summer to extend the period during which they have access to fruits, as many cervids in mountainous environments do, using vertical migration to follow plant phenology (Oosenbrug & Theberge, 1980; Myrnerud *et al.*, 2001; Pettorelli *et al.*, 2005). Also, bears selected land cover types in autumn with the highest potential fruit mass (*i.e.*, clearcut 5–20 y old and natural disturbance) and sites receiving low solar irradiation, where plant phenology could be delayed (Jeník & Rejmánek, 1969).

Large-scale bear movements seen in our study area (Mosnier *et al.*, 2008) probably resulted from the complex choices made by bears in response to the unproductive environment, including seasonal altitudinal movements and changes in land cover types selected. Such behaviour likely ensures resource availability throughout the year (Klenner, 1987). Study of space-use patterns (*i.e.*, home-range distribution) showed an absence of territoriality in this bear population (Mosnier *et al.*, 2008), implying that individuals could range freely to find the best conditions available. Nevertheless, although our results showed that black bears have developed specific adaptations to the unproductive boreal biome, bears are less abundant here than in southern regions (Jolicoeur, 2004). Human activities, in particular forestry practices, however, could increase overall habitat quality for bears and contribute to growth of bear populations in the boreal forest (Lamontagne, Jolicoeur & Lefort, 2006; Brodeur, 2007).

IMPLICATIONS

Black bears, along with coyotes (*Canis latrans*), are considered to be the main predators of calves of the endangered population of Gaspé caribou (Crête & Desrosiers, 1995). This population is generally restricted to areas above 700 m, which are mainly located inside the Gaspésie Conservation Park. Contrary to the results of Boileau *et al.* (1994) suggesting a spatial (altitudinal) segregation between black bears and caribou, we showed in this study that black bears used high elevations during spring and selected the barren and mature coniferous land cover types that are also preferred by caribou (Mosnier *et al.*, 2003). Boileau *et al.* (1994) also suggested that bear–caribou conflicts should diminish as coniferous stands mature because forestry activities in the park ceased in 1977. However, we found bears using the summits in spring selected stands resulting from clearcutting practices outside the park in summer or autumn. Even though we did not find any caribou remains in the bear diet, bear presence during the calving period could result in opportunistic predation on caribou calves (Ballard, 1994; Crête & Desrosiers, 1995). A habitat management plan has already been established to maintain suitable conditions for caribou in several sectors around the Gaspésie Conservation Park (Champagne *et al.*, 1999). Results of this study provide additional information and suggest clearcutting practices near the caribou range should be avoided since clearcuts result in increased fruit abundance and thus improve habitat quality for bears. If logging must be carried out, partial cutting should be preferred to clearcuts because bears avoided partial cuts in all seasons. Because coyotes also benefit from clearcuts (Boisjoly, 2007), a habitat management plan involving partial cutting should impact both predators of caribou.

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