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Source: Journal of Mammalogy, 89(4) : 1001-1011

Published By: American Society of Mammalogists

URL: https://doi.org/10.1644/07-MAMM-A-192.1

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Journal of Mammalogy, 89(4):1001–1011, 2008

PREY SELECTION BY MARINE-COASTAL RIVER OTTERS (*LONTRA CANADENSIS*) IN NEWFOUNDLAND, CANADA

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Previous studies have suggested that diets of river otters (*Lontra canadensis*) vary in response to seasonal shifts in prey availability, and that they select slowly moving fish of moderate size. To test these assumptions for marine-coastal river otters in Newfoundland, Canada, we reconstructed diets and estimated body length of important fish prey through analysis of otoliths and other hard parts recovered from scats collected in Bonavista and Placentia bays. Diet of otters in Bonavista Bay also was compared with the species and size composition of the nearshore fish community, as determined by concurrent beach-seine sampling. Diets were qualitatively similar but quantitatively different between bays. Otters consumed proportionally more cunner (*Tautogolabrus adspersus*) and stickleback (Gasterosteidae) in Placentia Bay, and more sculpin (Cottidae) and cod (*Gadus*) in Bonavista Bay. Flounder (*Pseudopleuronectes americanus*) was important in both bays, based on biomass, because individual fish in the diet were large. Fish-community composition in Bonavista Bay varied seasonally, a pattern that was not reflected in the diet, suggesting active selection of fish prey by otters. Slow-swimming fish (sculpin, flounder, and ocean pout [*Macrozoarces americanus*]/rock gunnel [*Pholis gunnellus*]) were overrepresented in the diet, and fast-swimming species (cod and hake [*Urophycis*]) were underrepresented. Otters also selected larger individuals within taxa. The lower limits at which size classes were incorporated into diet varied across fish species, and may reflect species differences in detectability by otters due to camouflage and behavior.

Key words: diet, feeding ecology, *Lontra canadensis*, Newfoundland, prey selection, river otter

North American river otters (*Lontra canadensis*; hereafter, otters) inhabit a wide variety of habitats in freshwater (wetland, river, and lakes) and coastal-marine environments, where they are exposed to many different prey species (Toweill and Tabor 1982). A number of studies designed to determine prey species of otters have been conducted, but have been carried out primarily in central and western North America (Ben-David et al. 1998, 2005; Bowyer et al. 1994, 2003; Dolloff 1993; Greer 1955; Larsen 1984; Reid et al. 1994; Ryder 1955; Stenson et al. 1984). Despite this work, key aspects of foraging ecology such as prey selection are not well understood for this species and are mainly speculative.

The diet of river otters varies seasonally and is assumed to reflect seasonal changes in availability of prey communities, particularly slow-moving, midsize prey (Greer 1955; Larsen 1984; Melquist and Hornocker 1983; Reid et al. 1994; Stenson et al. 1984; Toweill and Tabor 1982). However, these hypotheses have never been tested. Evidence of selection for larger and slower fish has been found for Eurasian otters (*Lutra lutra*) in experimental studies by Erlinge (1968). Recent field studies examining diets of Eurasian otters also have revealed that this species is an opportunistic piscivore that modifies its diet relative to prey availability (Lanszki et al. 2001; Polednik et al. 2004; Taastrom and Jacobsen 1999). Knowledge of the feeding ecology of Eurasian otters is useful for assessing that of river otters; however, direct inference may be questionable because of differences between the 2 species (e.g., in life history).

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In this study, we investigated diets of river otters from 2 geographically separated marine-coastal regions of Newfoundland, Canada, to determine whether regional variation in diet occurs. We also used data on nearshore fish communities in 1 of our regions to evaluate 3 hypotheses: seasonal variation in diet reflects prey availability in nearshore fish communities; slow-swimming prey species are captured more easily, hence are overrepresented in the diet; and otters select large prey, among those available.

Materials and Methods

Study area.—We sampled feces (scats) of river otters from sites in Bonavista Bay and Placentia Bay, in Newfoundland, Canada (Fig. 1). These bays are characterized by rocky headlands, convoluted shorelines, and numerous islands. Bonavista Bay is influenced by pack ice during late winter and early spring. In contrast, the more southerly Placentia Bay has ice cover infrequently, and the water is generally warmer for much of the year (Craig and Colbourne 2004).

Collections and sample preparation.—We collected scats from 19 latrine sites (Bonavista Bay: 12; Placentia Bay: 7) from June 2001 to May 2002 (Fig. 1). Each site was visited at approximately monthly intervals to limit temporal autocorrelation (Carss and Parkinson 1996). Fresh scats were collected and individually bagged; other residues and deteriorating scats were destroyed to avoid confusion during subsequent sampling. Collection protocols were in accordance with guidelines approved by the American Society of Mammalogists (Gannon et al. 2007).

Samples were kept frozen until examination. Each sample was placed in a glass jar, soaked in water and detergent for 2–3 days, and then shaken to loosen undigested remains from mucilaginous material (Beja 1997). Samples were then washed through a series of nested sieves of decreasing mesh size (3.00 to 0.25 mm). Hard parts were separated, air-dried, and stored until further analysis.

Sagittal otoliths of bony fish are taxa-specific, and their size is positively correlated with age and body size (Härkönen 1986; Hunt 1992; Lidster et al. 1994). Using the otoliths found in scats, we determined the abundance of fish taxa consumed, relative frequencies of occurrence of different fish taxa (number of scats containing species *i*, divided by total number of scats), and the estimated body length and mass of ingested fish. Otoliths were identified to the lowest taxonomic level possible (common and scientific names follow Scott and Scott [1988]; Table 1). Two taxa (ocean pout [*Macrozoarces americanus*] and rock gunnel [*Pholis gunnellus*]; hereafter, ocean pout/rock gunnel) were difficult to distinguish from otoliths, so were lumped for analysis. Otoliths that are partly digested can lead to underestimates of fish size, so otoliths were graded following Tollit et al. (1997): class 1, undigested to slightly digested; class 2, moderately digested; and class 3, highly digested. The degree of digestion was based upon the amount of edge wear and loss of structural detail that had occurred. Class 1 otoliths showed no obvious signs of digestion, and sharp features were maintained. Class 2 otoliths exhibited slight indications of wear, but features were distinct and easily recognized. Class 3 otoliths exhibited smoothing or reduction of some edges and loss of surface features. We limited estimation of body size of fish to using otoliths from class 1 and class 2 only.

To enumerate prey items, otoliths within each scat were paired as left- or right-sided within taxa; the greater number of left or right sides was taken as the minimal number of fish represented for that taxon. Otoliths of sticklebacks (Gasterosteidae) could not be differentiated by side because they were too small (<0.8 mm). For these species, the total number of otoliths was halved to estimate the number of fish consumed. Otoliths were measured randomly, and every 2nd measurement was assumed to represent the length of the fish consumed. An image-analysis system was used to measure otolith length to the nearest 0.01 mm (Lawson et al. 1995). Otoliths > 3 mm in length were measured by hand to the nearest 0.01 mm with digital calipers. Regression equations, relating otolith length to fish length and mass, were used to estimate the length and weight of fish consumed (Benoit and Bowen 1990; Dolloff 1993; Härkönen 1986; Hunt 1992; Lawson et al. 1995; Lidster et al. 1994; Stenson and Perry 2001). When possible, regressions based on local populations were used. Unmeasured class 3 otoliths were included in biomass calculations by applying size frequencies of class 1 and 2 otoliths for a particular taxon. Nonfish food items identified from hard parts (carapace, hair, bone, shell, beak, berry rind, and seed) were recorded as present or absent.

We investigated prey selectivity in our Bonavista Bay study area by comparing proportionate representation of prey taxa in scats with the composition of fish samples obtained from a long-term nearshore fish community monitoring program (Gregory et al. 2006). We used a 25-m demersal seine net with 19-mm stretched mesh size. Nets were set 55 m from shore from a 6-m boat, and hauled by 2 people standing 16 m apart on shore. The seine sampled an area of ~880 m^2 at each site and collected fish up to 2 m off the bottom. This technique has a capture efficiency of ~95% (Gotceitas et al. 1997). Nine sites within Bonavista Bay (Fig. 1) were sampled biweekly through the period of scat collection, except for December 2001 through April 2002. Seine samples were only obtained for a portion of the scat collection area. Therefore, only scat samples that were geographically and temporally similar (9 latrine sites and 7 temporal periods: July, August, September, early October, late October, November, and May) were included in this analysis. Collections of scats preceded fish sampling by 4 days on average (range 1–8 days).

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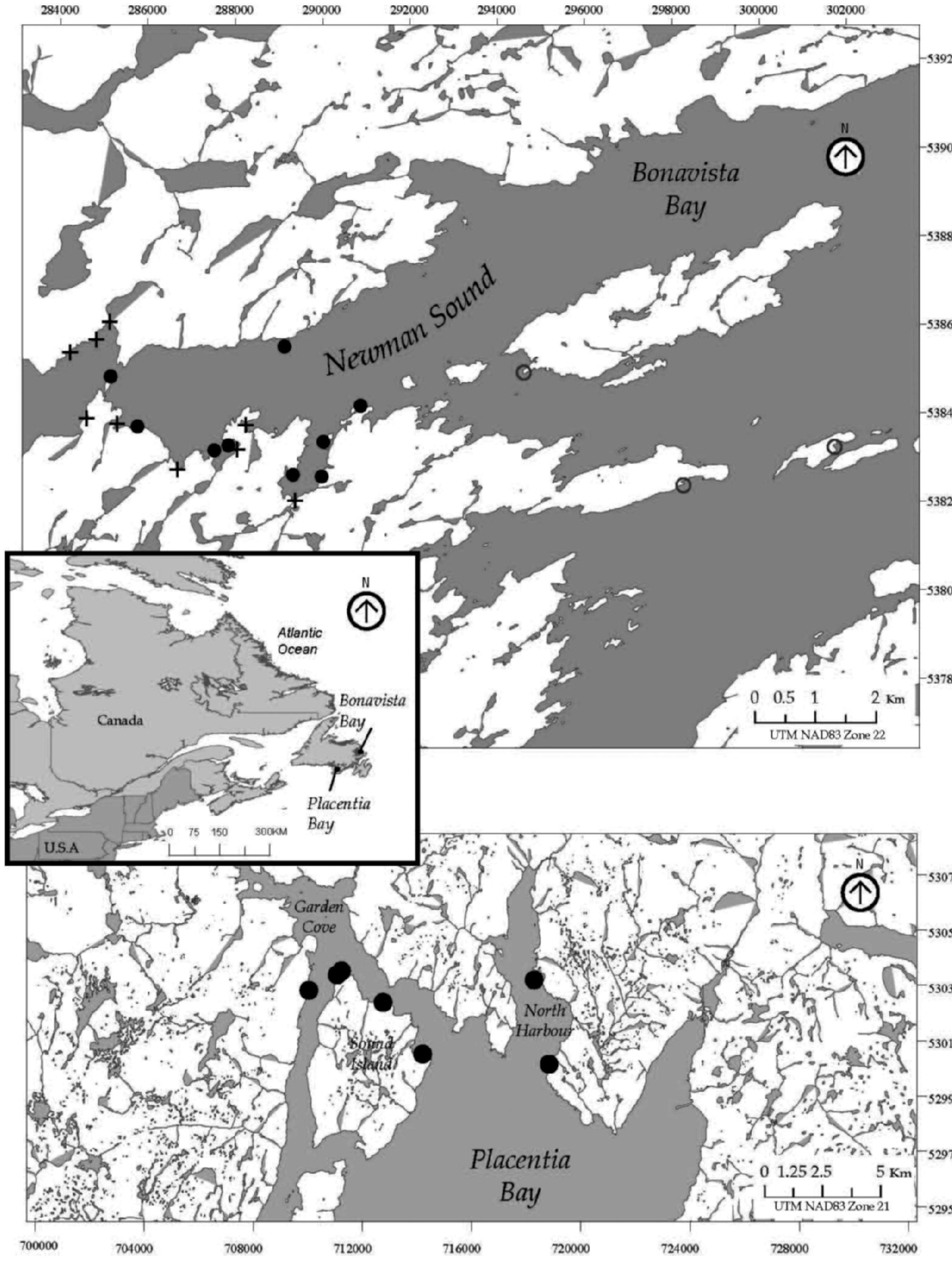
Fig. 1.—Locations of sampled latrine sites (circles) of river otters (*Lontra canadensis*) and fish-community sampling sites (crosses) in Newman Sound, Bonavista Bay, Newfoundland, Canada. Open circles represent latrine sites that were used in interbay comparisons but not in analyses of prey selection.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Statistical analysis.—To reduce spatial autocorrelation, data from all sites were pooled for each collection period (Carss 1995). We used the Bray–Curtis index (Bray and Curtis 1957) to analyze community similarity and dissimilarity in proportional abundance and biomass of prey species in diets of otters of both bays, and in seine collections of Bonavista Bay. Prey items that typified (i.e., contributed most to within-bay similarity values) and discriminated (i.e., contributed most to dissimilarity values of sites in different bays) diets of otters in each bay were determined using SIMPER (PRIMER version 6; PRIMER-E Ltd., Lutton, Ivybridge, United Kingdom). The SIMPER method evaluates the contribution of each prey species to Bray–Curtis similarity values for pairs of sites within and among groups. Statistical differences were evaluated through analysis of similarities (ANOSIM; PRIMER version 6; 999 permutations), a nonparametric permutation procedure (Clarke and Green 1988) comparable to analysis of variance (ANOVA). Interbay differences in length between prey types in the otter scats were assessed with ANOVA. SIMPER also was used to compare taxonomic composition of scat and seine samples. Bray–Curtis similarities of diet composition and nearshore fish communities were assessed for seasonal trends with an index of multivariate seriation (Clarke et al. 1993), and evaluated for statistical significance using a permutation test of Spearman rank-correlation coefficients (RELATE algorithm in PRIMER version 6; 999 permutations).

The hypothesis that otters select prey according to prey swimming ability was assessed in Bonavista Bay by grouping fish as relatively slow (sculpin [Cottidae], ocean pout/rock gunnel, and winter flounder [*Pseudopleuronectes americanus*; hereafter, flounder]) or relatively fast (cod [*Gadus*] and hake [*Urophycis tenuis*]) swimmers. Each period of scat collection was paired with the most recent fish survey. We fitted a log-linear model with 3 categorical variables to assess associations of prey prevalence with sampling method (scats or seines), swimming-speed groupings (slow and fast), and sampling times. Diet selection based on swimming-speed groupings would be supported if significant interactions between sampling method and swimming-speed groupings were detected.

In Bonavista Bay, the lengths of species abundant in the seine samples (cod, sculpin, cunner [*Tautogolabrus adspersus*], and flounder) were compared with the estimated lengths derived from otoliths. Ocean pout/rock gunnel was not included because there was no variation in length (all individuals fell within 1 size category) in both the diet and the seine samples. The relative occurrences of prey taxa were pooled in 5-cm length classes for both availability and diet. Pairwise differences (Euclidean distance) of length-frequency curves were analyzed with the ANOSIM routine in PRIMER (version 6; 999 permutations) to compare length classes within species.

RESULTS

Dietary differences between bays.—We examined 458 scats from Bonavista Bay and 353 from Placentia Bay. Most (>95%) otoliths could be identified and the proportion of usable otoliths (i.e., slightly or only moderately digested) was high, averaging 94% across fish taxa (minimum = 75%, for redfish [*Sebastes*]). Of these, most were only slightly digested (cunner: 76%; sculpin: 76%; cod: 46%; flounder: 14%). Scats were most abundant in Bonavista Bay from October to May, but varied little through the year in Placentia Bay, except for a peak in June. In both locations, fish were the dominant prey based upon frequency of occurrence (Bonavista Bay: 76%; Placentia Bay: 72%). Relative abundance of invertebrates in scats was similar in both locations, with molluscs being most important, followed by crustaceans, polychaetes, and echinoderms (Table 1).

Most fish identified in scats belonged to a small number of taxa in both study locations: sculpin, cod, cunner, ocean pout/rock gunnel, stickleback, and flounder accounted for >70% of the fish diet in each location (Table 1). Nevertheless, proportions of individual fish taxa in the diet differed between bays (ANOSIM: Global $R = 0.54$, $P = 0.001$; Table 2; Fig. 2). Differences in the abundance of 4 prey taxa contributed to ~80% of prey dissimilarity. Of these 4 taxa, cod and sculpin were most abundant in Bonavista Bay and stickleback and cunner were most abundant in Placentia Bay (Table 3).

Differences in biomass between bays also were significant, but less distinct than differences in abundance (ANOSIM: Global $R = 0.315$, $P = 0.001$). For Bonavista Bay, flounder, cod, sculpin, and cunner (in order of importance) defined intake of biomass, whereas for Placentia Bay, biomass was defined by cunner, flounder, and sculpin (Table 2). Dissimilarity in diet biomass between the 2 bays was driven by flounder, cunner, cod, and sculpin, of which all but cunner were in relatively higher proportions in Bonavista Bay (Table 3).

Some fish had small differences in size between bays. Cod, cunner, and flounder were significantly smaller in Placentia Bay (ANOVA: cod: $F = 11.2$, $d.f. = 1, 547$, $P < 0.001$; cunner: $F = 71.7$, $d.f. = 1, 797$, $P < 0.001$; flounder: $F = 30.9$, $d.f. = 1, 268$, $P < 0.001$), and sculpin and stickleback were significantly larger (ANOVA: sculpin: $F = 13.1$, $d.f. = 1, 1{,}058$, $P < 0.001$; stickleback: $F = 87.8$, $d.f. = 1, 1{,}082$, $P < 0.001$). Ocean pout/rock gunnel did not differ in size (ANOVA: $F = 0.6$, $d.f. = 1, 669$, $P = 0.45$).

Prey selection at Bonavista Bay.—Abundance of taxa in otter diet differed significantly from prey availability (ANOSIM; Global $R = 0.717$; $P = 0.003$). Most (70%) of the observed dissimilarity between proportional abundance in scats and seines was due to differences in cod, sculpin, ocean pout/rock gunnel, and cunner (Table 4). Biomass also differed significantly between diet and availability (ANOSIM: Global $R = 0.363$, $P = 0.013$). However, dissimilarity was due mainly to flounder, which contributed 31% to dissimilarity (Table 3). Considered together, 3 taxa (flounder, cunner, and cod) accounted for 80% of observed dissimilarity in biomass between diet and availability.

Seasonal trends.—Proportions of prey taxa varied over the 7 collection periods (ANOSIM test: Global $R = 0.717$, $P = 0.003$). In Bonavista Bay, this variation was reflected in a temporal, directional shift in fish community structure for seine samples (Fig. 3; RELATE: $\rho = 0.684$, $P < 0.001$); however, this pattern of variation was not evident in the diets of

TABLE 1.—Relative frequency of occurrence (%) of prey of river otters (*Lontra canadensis*) in Bonavista Bay and Placentia Bay, Newfoundland, Canada, as determined by scat analysis. Common and scientific names follow Scott and Scott (1988).

Prey item	Bonavista Bay ($n = 458$)	Placentia Bay ($n = 353$)
Fish	75.5	71.8
Sculpin (Cottidae)	23.2	12.9
Fourhorn sculpin (*Myoxocephalus quadricornis*)	0.1	0
Hookear sculpin (*Artediellus*)[a]	0.6	0.2
Arctic staghorn (*Gymnocanthus tricuspis*)	4.3	1.1
Shorthorn sculpin (*Myoxocephalus scorpius*)	18.2	11.6
Salmonidae	0.9	0.3
Brook trout (*Salvelinus fontinalis*)	0.8	0.1
Atlantic salmon (*Salmo salar*)	0.1	0.2
Gadidae	16.2	5.1
Arctic cod (*Boreogadus saida*)	0.4	0
Cod (*Gadus*)[b]	15.3	4.7
Hake (*Urophycis tenuis*)	0.5	0.3
Capelin (*Mallotus villosus*)	1.1	0.3
Atlantic herring (*Clupea harengus*)	0.1	0
Cunner (*Tautogolabrus adspersus*)	6.4	19.5
Ocean pout/rock gunnel (*Macrozoarces americanus*/*Pholis gunnellus*)	13.6	9.7
Redfish (*Sebastes*)	0	0.4
American shad (*Alosa sapidissima*)	0.4	0.1
Stickleback (Gasterosteidae)	2.7	14.8
Winter flounder (*Pseudopleuronectes americanus*)	10.8	8.2
Starry skate (*Raja radiata*)	0.5	0.9
Invertebrates	24.0	27.4
Mollusca	7.9	10.2
Crustacea	4.5	9.2
Polychaete	3.9	3.7
Echinoderm	2.7	2.8
Other invertebrates	4.8	1.4
Mammals	0.1	0
Masked shrew (*Sorex cinereus*)	0.1	0

[a] Otoliths of Atlantic hookear sculpin (*Artediellus atlanticus*) and snowflake hookear sculpin (*Artediellus uncinatus*) were indistinguishable.

[b] Otoliths of Atlantic cod (*Gadus morhua*) and Greenland cod (*G. ogac*) were indistinguishable.

otters in either Bonavista (RELATE: $\rho = 0.358$, $P = 0.063$) or Placentia Bay (RELATE: $\rho = 0.094$, $P = 0.305$). Nevertheless, seasonal differences were apparent for some prey taxa in scats. For example, cunner were absent or rare in scats collected from November through May (Fig. 2). A similar but weaker result was obtained for biomass (Fig. 3). Seasonality in biomass was evident in seine samples from Bonavista Bay (RELATE: $\rho = 0.729$, $P = 0.001$), but not for scat samples (RELATE: $\rho = 0.042$, $P = 0.402$).

Swimming mode.—The 3-way interaction between sampling method (seine and scat samples), swimming speed, and sampling time was significant ($\chi^2 = 349.4$, *d.f.* = 6, $P < 0.001$), suggesting that the strength of swimming-speed selection by otters varied across sampling periods. We then explored the 2-way interactions between swimming speed of prey and their prevalence in the diet of otters and in seines for each time period with separate (Bonferonni-corrected) chi-square tests. Otters showed significant selection for slow-swimming fish in all samples (all $\chi^2 > 11.3$, *d.f.* = 1, $P < 0.001$).

Prey size.—For each fish taxon in Bonavista Bay, more large individuals occurred in scats relative to seine samples (Fig. 4). Taxon-specific size selection by otters was observed. For example, cod > 10 cm in length were proportionally more common in scats than in seine samples, whereas flounder became more prevalent in scats at lengths > 25 cm. Size-selection limits were intermediate for cunner and sculpin. Cod and sculpin varied seasonally in size in both scats and seine samples (ANOSIM: cod: Global $R = 0.963$, $P = 0.001$; sculpin: Global $R = 0.635$, $P = 0.004$). Sample sizes for cunner and flounder were too small to test.

DISCUSSION

Fish dominated the diet of river otters in coastal Newfoundland, consistent with the trend throughout the species' range (Ben-David et al. 1998, 2005; Bowyer et al. 1994, 2003; Dolloff 1993; Greer 1955; Larsen 1984; Melquist and Hornocker 1983; Reid et al. 1994; Ryder 1955; Stenson et al. 1984). Otters in Bonavista Bay consumed most species present, as in freshwater systems (Reid et al. 1994). However, almost all prey species were marine, despite the presence of several fish-bearing freshwater systems nearby. Similarly, Bowyer et al. (1994) noted that freshwater and anadromous fish were rare in the diet of Alaskan marine-coastal otters, as did Heggberget and Moseid (1994) for marine-coastal Eurasian otters. Bowyer et al. (2003) observed that only 6 of 55 marine-captured river otters in Alaska were relocated in freshwater systems, indicating that coastal otters in Alaska forage predominantly in marine habitats.

Regional differences.—Marine-coastal river otters in 2 regions of Newfoundland preyed on several common species, with demersal species being predominant in abundance and biomass. The tendency for otters to prey on demersal fish has been documented in the North Pacific (Ben-David et al. 2005; Bowyer et al. 1994, 2003) and in Europe (Kruuk 1995). Despite this general similarity among bays in our study, diet in Bonavista and Placentia bays differed substantially in proportional representation of individual prey species.

The importance of prey species in the diet differed between the measures of abundance and biomass. Small prey items, such as stickleback and ocean pout/rock gunnel, were important in defining prey abundance in diets of otters. In contrast, flounder was unimportant in abundance, but was the most prevalent in biomass in both bays.

Marine-coastal otters are capable of switching foraging strategies according to time of year, prey availability, sex, and reproductive status (Blundell et al. 2002). Differences in diet between bays in this study support the idea that otters adapt to changing foraging conditions (Greer 1955; Reid et al. 1994). The cold Labrador Current influences Bonavista Bay, and water temperatures are consistently colder there than in Placentia Bay, which is influenced by the Gulf of St. Lawrence.

TABLE 2.—The proportional abundance and biomass of prey in the diet of river otters (*Lontra canadensis*) in Bonavista Bay and Placentia Bay, Newfoundland, Canada, from July 2001 to May 2002, as determined by scat analysis. Means and contributions to similarity are shown for species in the top 90% of similarity in abundance and biomass. NA = not applicable.

	Diet structure			
	Abundance		Biomass	
Species	% abundance ($\bar{X}$)	Similarity (% contribution)	% biomass ($\bar{X}$)	Similarity (% contribution)
Bonavista Bay				
Sculpin	33.7	39.7	17.2	17.5
Ocean pout/rock gunnel	18.4	20.5		
Cod	17.9	19.1	19.7	18.7
Cunner	8.8	5.5	14.0	9.5
Flounder	5.1	5.5	43.6	52.1
Placentia Bay				
Stickleback	39.1	43.9		
Cunner	31.6	30.2	40.5	46.3
Ocean pout/rock gunnel	9.6	10.9		
Sculpin	11.0	8.3	8.3	6.3
Winter flounder	NA	NA	34.4	41.2

TABLE 3.—Interbay differences in proportional abundance and biomass of prey species in diet of river otters (*Lontra canadensis*) in Bonavista Bay and Placentia Bay, Newfoundland, Canada, from July 2001 to May 2002, as determined by scat analysis. Prey-taxa contributions to Bray–Curtis dissimilarity between bays also are provided (highest dissimilarity contributions indicate taxa that best discriminate diets of otters in these bays). Species in the top 90% (cumulative) of similarity in abundance or biomass are included.

Species	Bonavista Bay	Placentia Bay	Dissimilarity (% contribution)
Abundance (%)			
Stickleback	9.2	39.1	26.8
Cunner	8.8	31.6	21.7
Sculpin	33.7	11.0	21.3
Cod	17.9	2.3	12.7
Ocean pout/rock gunnel	18.4	9.6	9.0
Biomass (%)			
Cunner	14.0	40.5	32.9
Flounder	43.6	34.4	20.9
Cod	19.7	5.5	17.3
Sculpin	17.2	8.3	13.0
Stickleback	0.6	6.6	6.5

This difference influences fish distribution, prey behavior, and prey vulnerability (Erlinge 1968; Rose et al. 2000). Cold water reduces the ability of ectothermic prey to escape from endothermic predators (Erlinge 1968; Rowe-Rowe 1977; Valdimarsson and Metcalfe 1998). For those prey species that become torpid in cold water and seek refuge, such as cunner (Scott and Scott 1988), cold water may reduce vulnerability to predators such as otters (Wise et al. 1981). Therefore, it is not surprising that species such as cunner, which are active in warm water, are more prevalent in the diet of otters in the warmer Placentia Bay.

Seasonal trends.—Diets of river otters in freshwater environments typically show seasonal patterns. Such patterns may result from seasonal depletion of certain prey species or life stages, which is less likely to occur in marine-coastal environments (Kruuk et al. 1988, 1993). Lack of seasonality in diets of otters in marine-coastal British Columbia has been interpreted as a reflection of uniform prey availability through the year (Stenson et al. 1984). We also found absent-to-weak seasonal trends in diet in our study of a marine-coastal population; however, in Newfoundland this occurs in the face of strong seasonality in prey availability. We interpret these findings to mean that otters in marine-coastal areas of Newfoundland actively selected prey based on fish availability, swimming speed, and size.

Swimming speed.—In our study, slow-swimming fish taxa were included in the diet of river otters more than expected based on availability, in contrast to fast-swimming taxa. Selection of fish in relation to swimming speed was 1st suggested in a captive study on Eurasian otters, and later confirmed in the wild (Erlinge 1968; Jacobsen 2005; Taastrom and Jacobsen 1999). This preference for slower species would be predicted from the perspective of optimal foraging, in which reduced chase times and higher capture rates are selected (Erlinge 1968). Nonetheless, in some circumstances, otters may target fast-swimming pelagic species. In the North Pacific, social otters seasonally apply cooperative foraging techniques to target energy-rich schooling pelagics (Ben-David et al. 2005; Blundell et al. 2002). However, such behavior has not been observed in our study area, where groups of otters are typically limited to 2 adults with young.

TABLE 4.—Differences between prey availability and prey consumed for diet of river otters (*Lontra canadensis*) in Newman Sound, Bonavista Bay, Newfoundland, Canada. Diet (from scat analysis) and availability (from beach-seines) are represented as mean proportional abundance and biomass per collection period. Prey-taxa contributions to Bray–Curtis dissimilarity between diet and availability also are provided (highest dissimilarity contributions indicate taxa that best discriminate diet and available prey). Species in the top 90% (cumulative) of dissimilarity are included.

Species	Diet	Seine	Dissimilarity (% contribution)
Abundance (%)			
Cod	13.9	48.0	27.0
Sculpin	33.2	5.3	21.0
Ocean pout/rock gunnel	19.7	4.2	11.6
Cunner	13.2	14.0	10.2
Stickleback	11.5	2.5	8.6
Hake	0.1	11.5	8.5
Atlantic herring	0	9.2	6.9
Biomass (%)			
Flounder	51.0	17.2	31.5
Cunner	18.7	34.6	28.3
Cod	15.0	27.6	20.6
Sculpin	14.4	8.1	7.5
Hake	0.04	6.5	1.1

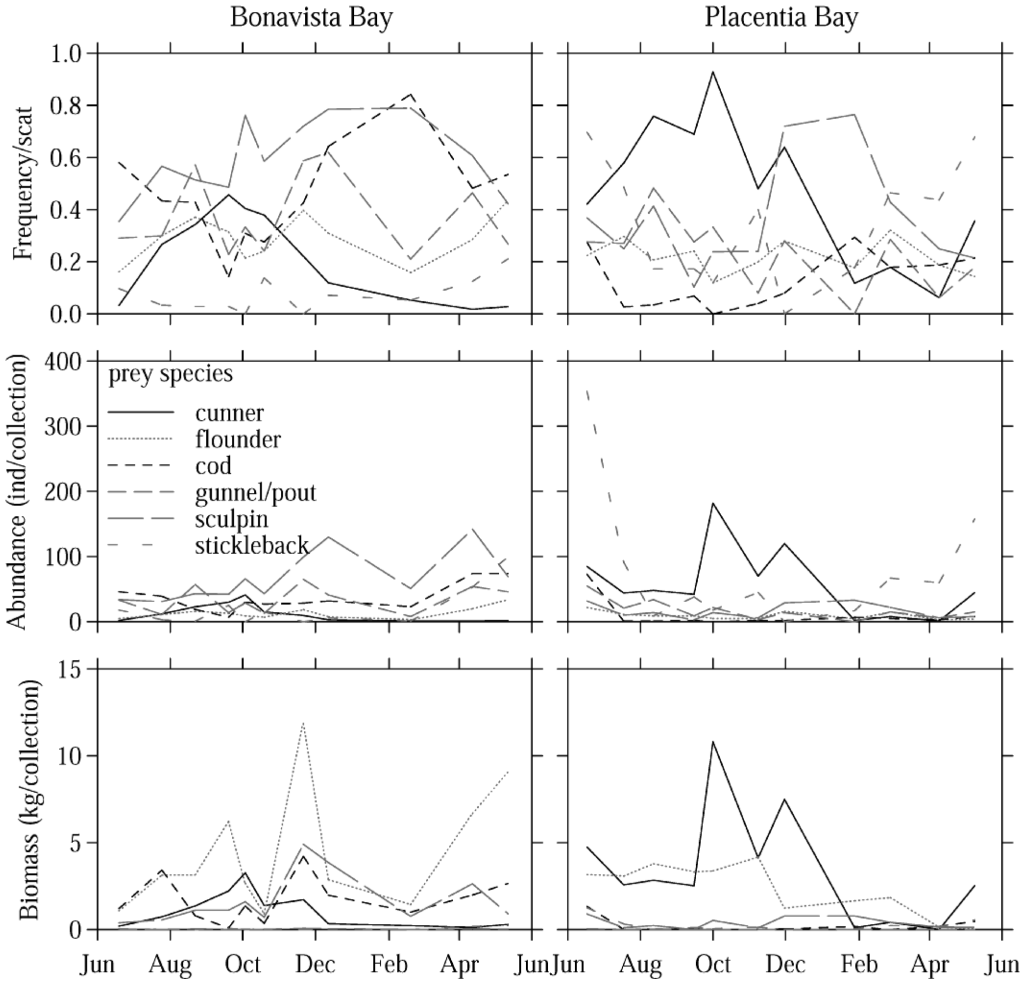

Fig. 2.—Frequency of occurrence (top panels), total abundance (middle panels), and biomass per collection period (bottom panels), of major prey species in the diet of river otters (*Lontra canadensis*) in Bonavista Bay and Placentia Bay, Newfoundland, Canada, June 2001 through May 2002.

Prey size.—We found strong evidence of prey-size selection in otters of Bonavista Bay. Otters began to prey selectively on body lengths > 10 cm for cod, > 15 cm for cunner and sculpin, and > 25 cm for flounder. Eurasian otters in Denmark tended to prey on fish 9–21 cm in length (Taastrom and Jacobsen 1999), although they also are known to include some species up to 40 cm in length (Jacobsen 2005). The size spectrum of available prey in our study was not great, but otters did not appear to be limited by large prey size. Swimming speed of fish generally increases with body length (Bainbridge 1958), which could make large fish more difficult to capture. However, this did not appear to regulate selection of large prey by otters in our study. In contrast, Lanszki et al. (2001) determined that Eurasian otters in Hungary had an upper prey-size limit at ~1 kg.

We found a clear lower size-selection limit for all key prey species in Bonavista Bay, although this varied across species. A lower limit of selected prey is expected because costs of pursuit, capture, and handling may not be justified by energy or nutrients acquired. Assuming equal swimming speed, species with the lower size-selection limit should contain more energy. However, a 15-cm-long cod has only three-fourths of the mass (Bowen and Harrison 1996; Lilly et al. 2000) and energy content (Lawson et al. 1995) of a flounder of the same length, yet maintains the lower size-selection limit.

Handling costs also could influence lower size-selection limit. Eurasian otters appear to prefer fish with soft integument over those with hard integument and spines (Heggberget and Moseid 1994). However, prey-selection patterns in our study do not appear to be strongly influenced by this factor. For example, cunner has a hard integument and a moderate lower size-selection limit, whereas flounder has a soft integument but the highest lower size-selection limit.

Finally, species differences in crypsis may explain lower size-selection limits (Gotceitas and Brown 1993). Cod and cunner are mobile and free-swimming (not strictly associated with the bottom), so likely are more conspicuous to otters than species that are more cryptic and less active (e.g., sculpin and flounder). This explanation fits our data best. Nonetheless, interactions between predator and prey are complex and involve several confounding factors, and it seems unlikely that crypsis by itself determines lower size limits of prey species (reviewed by Endler 1991). However, uncovering the mechanism behind size-selection limits would provide valuable insight into modeling diet choice by predators.

Despite selection for larger individuals, otters ingested substantial quantities of small prey. Some, like stickleback, could have been taken while in schools; however, others, such as ocean pout/rock gunnel, live a more solitary lifestyle. Consumption of small fish (<10 cm) by otters is not uncommon and has been reported in inland areas (Dolloff 1993)—albeit in an area where few large fish were available. Hungry otters are less discriminating (Erlinge 1968) and they likely rely on smaller, less-preferred prey to supplement their diet in the wild.

Sampling considerations.—Our study appears to be the 1st that compares diets of otters with local prey availability, considering both prey species and size. As with any fish-sampling method, the seine technique has biases. Seines are active gear, collect a high proportion of available fish (Gotceitas et al. 1997), and are effective for a broad range of species in habitats and depths (Kruuk and Moorhouse 1991; Nolet et al. 1993) preferred by foraging marine-coastal otters. At 1st glance, the seine should be less effective in sampling benthic fish that rely on crypsis (e.g., sculpin and flounder) when threatened. However, in past practice we have observed that these species tend to break from cover and swim up from the bottom as the lead rope of the seine approaches, and are entrapped within the net. Even fast-swimming pelagic species are captured on occasion in large numbers, consistent with their occurrence (R. S. Gregory, in litt.). Furthermore, our estimates of prey availability are supported by studies that have used other techniques (Cote et al. 2001; Linehan et al. 2001). Thus, we feel that sampling biases associated with seining have not affected the patterns we observed.

A consequence of the use of data on fish availability from a long-term study is that latrine sites and fish-collection sites did not directly overlap. However, it is unlikely that this consideration would affect conclusions regarding seasonal trends, because the seasonality of fish communities occurs at scales larger than the study area (e.g., Cote et al. 2004). Potential size differences in prey between latrine sites and fish-collection sites also are unlikely to influence our conclusions. Otter latrines in other coastal areas are linked to highly structured habitats (Ben-David et al. 2005). Small fish also seek habitat structure in the presence of predators (e.g., Gotceitas and Brown 1993; Laurel et al. 2003) and thus this bias would underestimate their prevalence in the nearshore, and by extension, the tendency for otters to select larger individuals.

Reconstructing prey sizes based on otoliths also carries methodological biases. Large, sturdy otoliths are likely to be overrepresented in feces because they are affected relatively little by digestion (Bowen 2000; Tollit et al. 1997). This would lead to overestimates of large individuals and species in the diet. We included only slightly and moderately digested otoliths in our study to reduce this bias. Tollit et al. (1997) graded the degree of digestion and provided grade-specific correction factors to mitigate such bias. They reported reductions in size for lightly and moderately digested otoliths as 10% and 26%, respectively. Correction factors were not incorporated in our analysis, but we believe this does not affect our findings. In fact, underestimating the size of cod and flounder (for which 54% and 86% of otoliths were at least moderately digested) would only strengthen our contention that otters select larger individuals of those taxa.

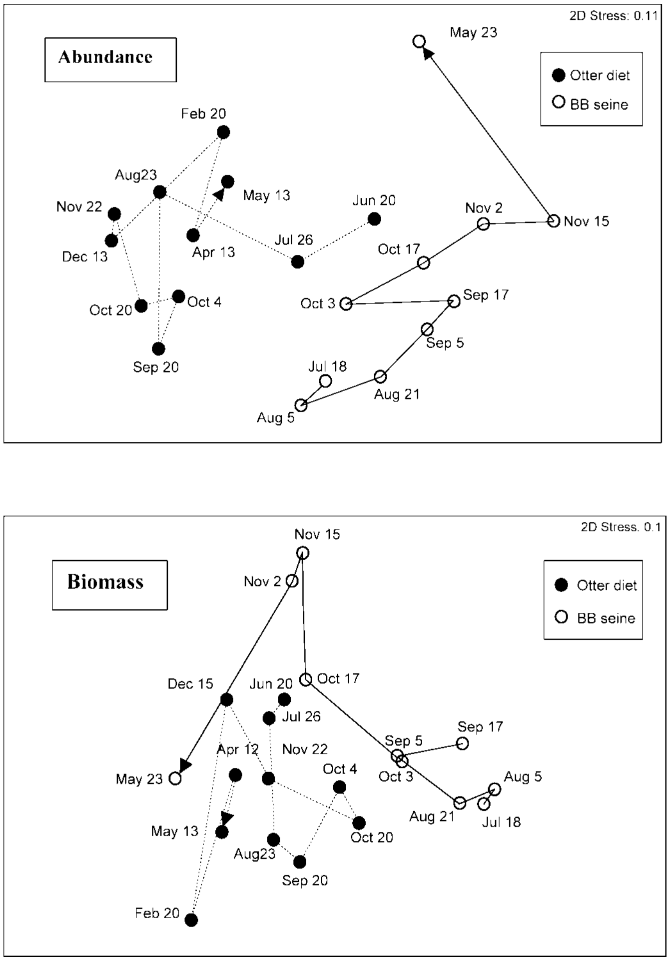

FIG. 3.—Nonparametric multidimensional scaling of Bray–Curtis similarity values for diet (abundance and biomass) of river otters (*Lontra canadensis*) versus available prey community (seine) in Bonavista Bay, Newfoundland, Canada. Proximity of points reflects community similarity.

Our study represents the 1st to describe feeding ecology of river otters in coastal areas of the Atlantic seaboard. It is also the 1st to empirically evaluate previous published assumptions of prey-selection criteria for this species. Although adaptable and incorporating a variety of prey in their diet, otters in coastal Newfoundland do not consume prey in a manner that mirrors seasonal trends in availability. Nonetheless, diet selection generally confirms speculation that otters prefer less-mobile and larger (i.e., midsized) prey among those available in the shallow coastal marine environment. Species-specific size selectivity for prey suggests that factors other than size (e.g., detectability and crypsis) also may play an important role in prey selection by river otters.

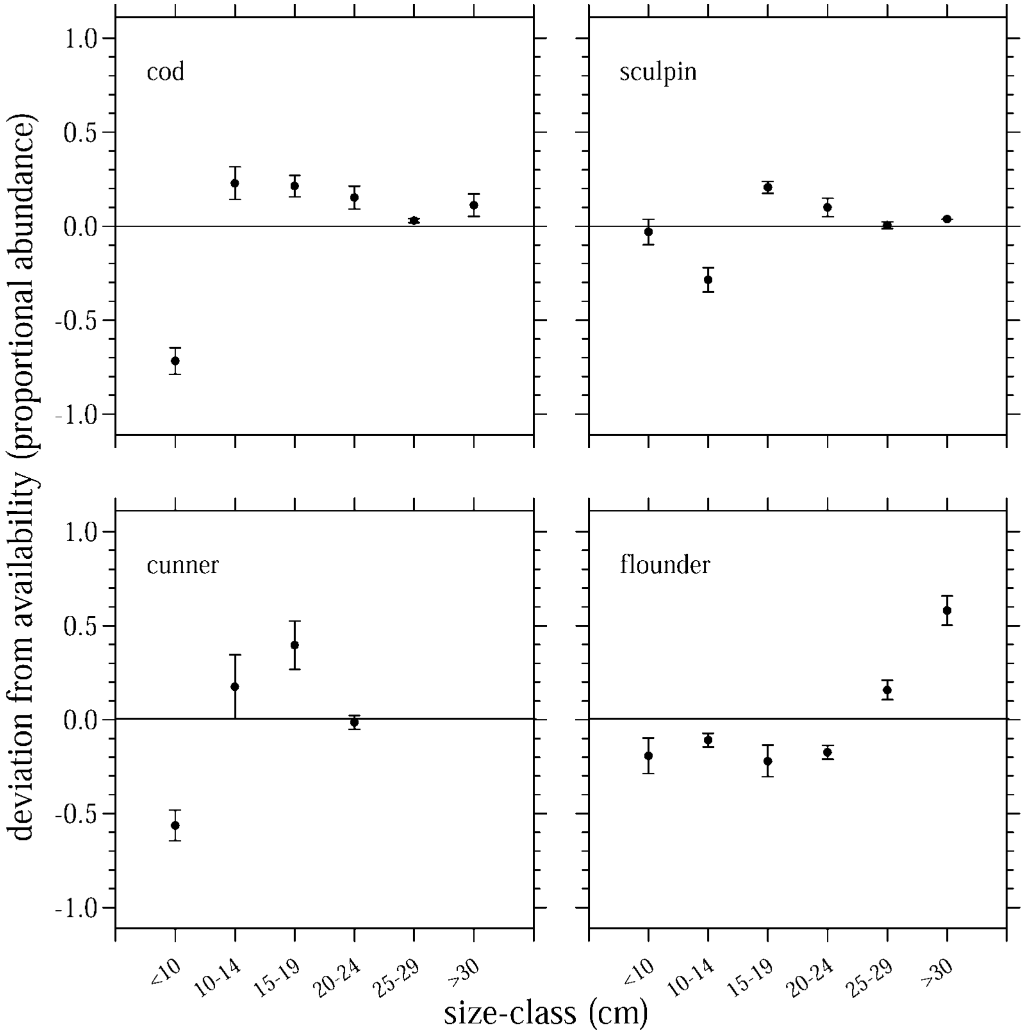

Fig. 4.—Prey-size selection by river otters (*Lontra canadensis*) in Newman Sound, Bonavista Bay, Newfoundland, Canada, from July 2001 to May 2002. Mean (bars = *SE*) differences in proportional abundance between paired diets of otters and beach-seine collections are shown. Points above the line indicate that prey were consumed at higher levels than they were available.

Acknowledgments

We thank the staff of Terra Nova National Park and the Newfoundland and Labrador Wildlife Division, Fisheries and Oceans Canada, the Heritage Foundation for Terra Nova National Park, and Memorial University for assistance with the fieldwork; D. McKinnon for help with analyzing scat samples; and Parks Canada and Fisheries and Oceans Canada (through its Environmental Sciences Strategic Research Fund) for financial support. E. Loder, M. McGrath, N. Burgess, M. Page, B. Clarke, and D. Kehler provided valuable assistance in the design and analysis of this project. Finally, we appreciate the contributions of the anonymous referees to this manuscript.

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Submitted 21 June 2007. Accepted 18 January 2008.

Associate Editor was Rodrigo A. Medellín.