



Research Article

# Spatiotemporal Variation in the Distribution of Potential Predators of a Resource Pulse: Black Bears and Caribou Calves in Newfoundland

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**ABSTRACT** Understanding spatiotemporal variability in prey accessibility is important for disentangling predator-prey interactions and is relevant to management interventions to reduce predation. Recently, caribou (*Rangifer tarandus*) in Newfoundland declined by 66%, with calf predation by black bears (*Ursus americanus*) implicated as a major proximate mechanism of the decline. Most predation occurs when calves are aggregated on calving grounds. We used telemetry data from 271 caribou and 45 black bears in 2 caribou herd ranges to examine spatial variability in calf accessibility, identify the distribution of potentially predatory bears, and assess the aggregative response of bears to the calf resource. We predicted whether a bear was a visitor to a calving ground during the calving season (a potentially predatory bear) based upon its sex, the herd range it occupied, its distance to the calving grounds, and the season. The distribution of potentially predatory bears and their degree of segregation from non-predatory bears varied seasonally. The probability of a bear visiting the calving grounds during calving decreased with increasing distance from the calving grounds, and was greater for males than for females in all seasons at distances beyond 2.4 km from the calving grounds. Residency time of bears increased in the calving grounds of 1 herd during calving, suggesting an aggregative response to neonates in that area. For both herds, the estimated distribution of potentially predatory bears was much larger than the calving grounds, illustrating that the relevant scale of predator-prey interactions may extend far beyond the area where lethal encounters occur. Our work highlights the value of examining spatiotemporal dynamics of predator movements prior to implementing ecosystem manipulations designed to reduce predation and provides a modeling framework that can be used to guide management interventions in systems with aggregated prey. © 2015 The Wildlife Society.

**KEY WORDS** aggregative response, black bear (*Ursus americanus*), calving grounds, caribou (*Rangifer tarandus*), carnivore management, neonates, Newfoundland, predator-prey interactions, predator reduction, ungulate conservation.

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Ecosystems periodically experience large influxes of food resources (pulsed resources) that elicit responses from the consumer communities in these systems (Ostfeld and Keesing 2000, Yang et al. 2010). Examples include population fluctuations of mast-consuming rodents (Wolff 1996), birds foraging on insect irruptions (Hogstad 2005), and terrestrial mammals scavenging marine subsidies (Rose and Polis 1998).

These resource pulses may alter species interactions, population dynamics, food webs, and communities, thus influencing ecosystem functioning (Yang et al. 2010). Species that are able to most effectively exploit pulsed resources are typically generalist consumers that can switch to alternative resources in the absence of a pulse or after the pulse has subsided (Ostfeld and Keesing 2000). These opportunistic generalists may respond to resource pulses functionally (Holling 1959) by increasing consumption rates of pulsed resources (Hogstad 2005) or numerically by increasing population growth (Wolff 1996) or moving into areas of pulsed resources (aggregative response; Hassell and May 1973, 1974). The synchronous birth of calves in ungulate populations provides a predictable and relatively stable seasonal resource pulse that may influence the dispersion and abundance of predators preying on them (Schwartz and Franzmann 1991). These dynamics are of considerable interest to wildlife scientists because of the potential effects of predation of neonates on population demographics (Gaillard et al. 1998).

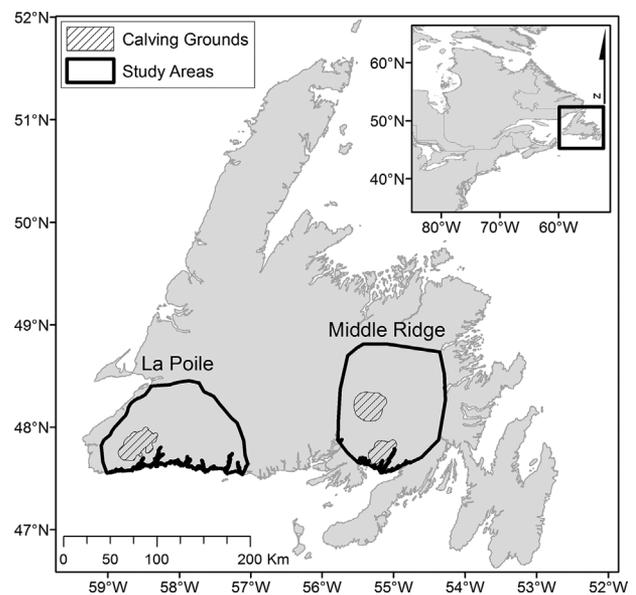
After several decades of rapid growth, the semi-migratory caribou (*Rangifer tarandus*) herds on the island of Newfoundland, Canada experienced a synchronous and precipitous population decline, decreasing from 94,000 to 32,000 individuals in the last 16 years (Weir et al. 2014). Recent investigations have implicated climatic and density-dependent effects as ultimate factors responsible for the population reduction (Bastille-Rousseau et al. 2013), with predation of calves likely the primary proximate factor (Weir et al. 2014). Since 2003, annual neonatal survival was estimated to be <10% in some years (Weir et al. 2014), with predation, principally by black bears (*Ursus americanus*) and coyotes (*Canis latrans*) accounting for >88% of all caribou calf mortalities (Mumma et al. 2014, Weir et al. 2014). The majority of parturient caribou in Newfoundland migrate to calving grounds at the end of May and remain aggregated in female-calf herds on the calving grounds during June (Bergerud 1974, Rayl et al. 2014) when most predation occurs (Lewis and Mahoney 2014). Predator-calf interactions vary both in space and time, especially for black bears less capable of capturing older, more mobile calves (Zager and Beecham 2006, Lewis and Mahoney 2014).

A persistent challenge facing wildlife scientists is identifying culpable predators in systems where calf predation is substantial (Mosnier et al. 2008). We developed a modeling framework to identify the distribution of black bears that visited the calving grounds during the calving season (potentially predatory bears) and document changes in the distribution of those bears throughout the year in 2 caribou herd ranges in Newfoundland. Given that male black bears have larger home ranges than female bears (Pelton 2003), we expected male bears to access the calving grounds from greater distances than female bears. Further, we hypothesized that the intensity of use of the calving grounds by bears would be influenced by the ephemeral abundance of caribou neonates in the calving grounds. We predicted that black bears would respond to the resource pulse of caribou calves by increasing their residency time in the calving grounds during the calving season.

## STUDY AREA

The island of Newfoundland (108,860 km<sup>2</sup>), Canada, is located in the North Atlantic Ocean (47°44'-N, 59°28'-W to 51°44'-N, 52°38'-W) and has a cool, maritime climate. We conducted research in 2 study areas on the island associated with the ranges of the La Poile (10,916 km<sup>2</sup>) and Middle Ridge (13,243 km<sup>2</sup>) caribou herds (Fig. 1). These areas were mostly roadless, with human settlements confined to the coast. The study areas were a mixture of bogs, heaths, barrens, and coniferous and mixed forests of balsam fir (*Abies balsamea*), black spruce (*Picea mariana*), tamarack (*Larix laricina*), mountain maple (*Acer spicatum*), birch (*Betula* spp.), and alder (*Alnus* spp.).

Caribou population estimates for both herds were derived from aerial surveys using a mark-resight design (Mahoney et al. 1998, Mahoney and Schaefer 2002). In 2011, the caribou population estimate for the La Poile herd was 4,200 ± 339 (SD), and was 10,445 ± 263 (SD) for the Middle Ridge herd in 2013 (G. Luther, Newfoundland and Labrador Department of Environment and Conservation, unpublished data). Most females from the Middle Ridge herd calved in an area called Middle Ridge North, but <5% used a second area called Middle Ridge South (Fifield et al. 2013). Previously, we used telemetry data from 52 adult female caribou (30 La Poile, 22 Middle Ridge) and 219 caribou calves (99 La Poile, 120 Middle Ridge) to identify the calving grounds of the La Poile and Middle Ridge herds; we found that the distribution of calves in the calving grounds was predictable in time and space across years, and we determined that most calves migrated from the calving grounds at the end of June (Rayl et al. 2014). We used the primary distribution of the composite calving ground delineations from Rayl et al. (2014) to describe the distribution of calves in La Poile (889 km<sup>2</sup>), Middle Ridge



**Figure 1.** We captured black bears in 2 areas associated with the range of the La Poile (11,252 km<sup>2</sup>) and Middle Ridge (13,369 km<sup>2</sup>) caribou herds, Newfoundland, Canada, 2008–2013. Note that females from the Middle Ridge herd calved in 2 areas (Middle Ridge North and Middle Ridge South).

North (867 km<sup>2</sup>), and Middle Ridge South (589 km<sup>2</sup>) from 20 May to 30 June (hereafter, calving grounds; Fig. 1).

## METHODS

### Bear Capture and Monitoring

We captured black bears throughout the range of both herds using Aldrich foot snares or by darting them from a helicopter during May–October 2008–2012 (2008–2010 in La Poile, 2008–2012 in Middle Ridge). We immobilized bears with a mixture of tiletamine-zolazepam administered intramuscularly with a CO<sub>2</sub>-powered pistol at a dosage of 4–7 mg/kg. We radiocollared 68 black bears >2 years of age with global positioning system (GPS) radiocollars (GPS 4400M, IridiumTrack3D, Lotek Wireless Inc., New Market, ON, Canada; G2110E, Advanced Telemetry Systems [ATS], Isanti, MN) that attempted a location every 1, 2, or 4 hours when bears were not denning, and we monitored them from 2008 to 2013 (33 F, 35 M, 146 bear-years, 130,039 locations). The Lotek GPS 4400M collars were deployed from 2008 to 2012 and were programmed to acquire a location every 4 hours from 1 April to 20 May and from 1 August to 31 December, and every 2 hours from 21 May to 31 July. The Lotek IridiumTrack3D collars were deployed from 2010 to 2012 and were programmed to acquire a location every hour from 1 April to 31 December. The ATS G2110E were deployed from 2011 to 2013 and were programmed to acquire a location every 4 hours from 1 April to 31 December. We experienced a high failure rate with the Lotek IridiumTrack3D collars (20 of 44 collars failed <60 days, 37 of 44 failed <1 yr) and the ATS G2110E collars (11 of 29 failed <60 days, 15 of 29 failed <1 yr). We recollared bears in their dens when snow conditions allowed, opportunistically when we recaptured them in foot snares, or by targeting them for recapture and darting them from the air. Animal capture and handling procedures conformed to guidelines established by the American Society of Mammalogists (Sikes et al. 2011) and were approved by the University of Massachusetts Amherst Institutional Animal Care and Use Committee (Protocol 2009-0047).

We defined 4 resource-based seasons. We classified den emergence (mean = 20 Apr) to 19 May as spring, a period when there were limited resources available. We considered 20 May to 30 June as the calving season; from 2008 to 2012, 78% (53 of 68 mortalities) of collared caribou calf mortalities in La Poile and Middle Ridge attributed to black bears occurred during this period (S. P. Mahoney, Newfoundland and Labrador Department of Environment and Conservation, unpublished data), 93% of which were within our calving ground delineations. We designated 1 July to 14 September as summer; in this season, green vegetation and soft mast were abundant. Finally, we defined 15 September to den entrance (mean = 28 Oct) as autumn, a period when soft mast availability peaked and then declined and all bears denning. We excluded seasonal data for individual bears on an annual basis when we had <15 days of telemetry data in a season.

An initial examination of the locations of bears revealed 2 distinct spatial distributions during the calving season

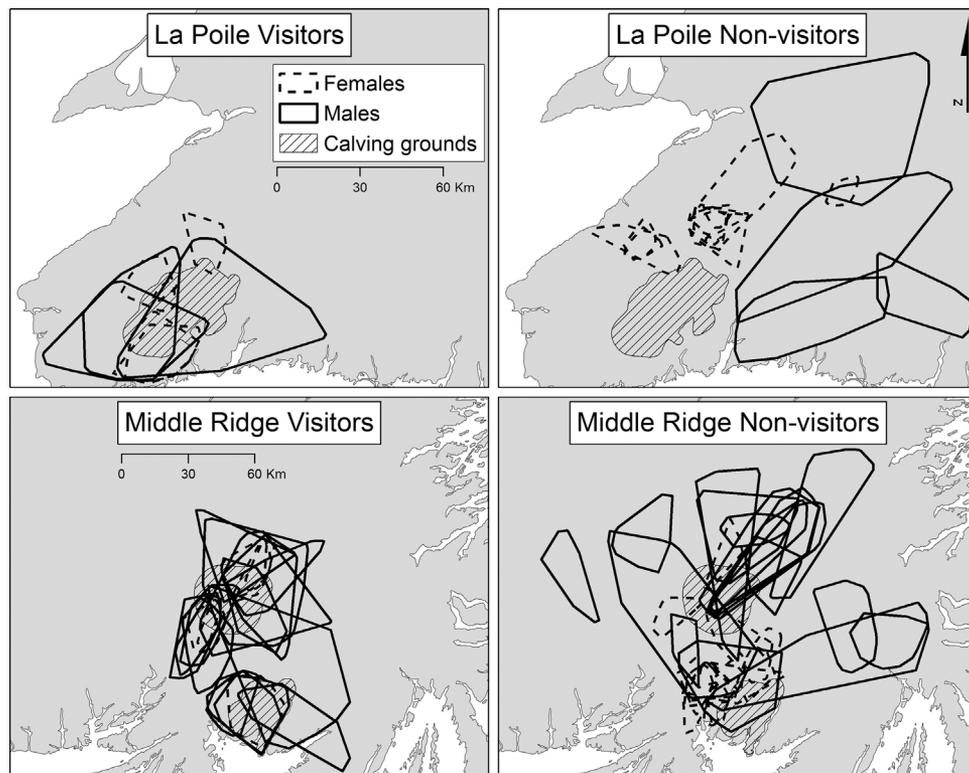
within the range of both caribou herds. Some bears were within the calving grounds during calving, whereas others were not. We classified bears annually in all seasons as either visitors (if they were located within the calving grounds >17% of the calving season in that year) or non-visitors (if they were located within the calving grounds <6.5% of the calving season in that year; Fig. 2). We used a cut-off of 6.5% to ensure that 6 bears that briefly spent time just inside the boundary of the calving grounds during the calving season were classified as non-visitors for those years and a cut-off of 17% because no bears spent between 6.5% and 17% of the calving season in the calving grounds. We excluded data from bear-years that could not be classified because they did not contain location data during calving ( $n=21$ ; large reduction due to collar malfunctions [see above]), and from bear-years when a diversionary feeding program in Middle Ridge South may have influenced bear movements ( $n=2$ ). As a result, our dataset included 45 black bears (20 F, 25 M, 74 bear-years, 83,716 locations; Supplemental Material Table S1). Although classification as a visitor did not indicate that a bear was preying on caribou calves, only visitors, or a subset of visitors (e.g., calf-consuming specialists; Ballard and Miller 1990), could be significant predators of calves from our focal herds because of the location and timing of most predation.

### Seasonal Models of Calving Ground Visitors

We used generalized estimating equations (GEEs; Liang and Zeger 1986) with a binomial error distribution and logit link function to predict whether a bear was a visitor (coded as 1) or non-visitor (coded as 0) in each season, based upon a bear's distance to the calving grounds, sex, caribou herd, and all 2-way interactions, with clusters defined as individual bears. The global GEEs took the form:

$$\begin{aligned} \text{logit}(P) = & \alpha + \beta_{\text{Distance}}^{x_{\text{Distance}}} + \beta_{\text{Sex}}^{x_{\text{Sex}}} + \beta_{\text{Herd}}^{x_{\text{Herd}}} \\ & + \beta_{\text{Distance} \times \text{Distance}}^{x_{\text{Distance}} \times x_{\text{Distance}}} + \beta_{\text{Distance} \times \text{Distance}}^{x_{\text{Distance}} \times x_{\text{Distance}}} \times \beta_{\text{Herd}}^{x_{\text{Herd}}} \\ & + \beta_{\text{Sex} \times \text{Sex}}^{x_{\text{Sex}} \times x_{\text{Sex}}} + \beta_{\text{Herd} \times \text{Herd}}^{x_{\text{Herd}} \times x_{\text{Herd}}}, \end{aligned}$$

where  $P$  represented the seasonal probability of a bear being a visitor,  $\alpha$  was the intercept, and  $\beta_u$  was the coefficient for variable  $x_u$ . We used the straight-line length between telemetry locations and the nearest border of a calving ground to calculate the distance of each location to the calving grounds, assigning all locations within the calving grounds a distance of 0. In Middle Ridge, we measured distances for individual visitors only to the particular calving ground (Middle Ridge North or Middle Ridge South) visited during calving, except in the case of 1 male visitor where we used the distance to the nearest border of either calving ground because that bear spent time in both calving grounds during calving. We used average daily distances calculated for each individual ( $n=9,649$ ) rather than distances from every telemetry point as our model input to reduce computation time. We used GEEs because both visitors and non-visitors often moved large distances away from or towards the calving grounds within a season, and GEEs allowed us to include this variation within our models, while also accounting for the lack of independence in repeated



**Figure 2.** Distribution of annual 100% minimum convex polygon home ranges of black bears designated as visitors or non-visitors in the ranges of the La Poile and Middle Ridge caribou herds, Newfoundland, 2008–2013.

distance measurements from the same individual (Liang and Zeger 1986).

Commonly used working correlation structures in GEEs include independence, exchangeability, or autoregressive (AR1; Fieberg et al. 2010). Although we attempted to fit GEEs using all 3 correlation structures, only models with an independence working correlation structure converged. An attractive characteristic of GEEs, however, is that their parameter estimates and empirical standard errors are robust to misspecification of the working correlation structure (Liang and Zeger 1986, Overall and Tonidandel 2004, Koper and Manseau 2009). We used a manual backward stepwise procedure to simplify global models until all variables were significant ( $P \leq 0.05$ ; Zuur et al. 2009). We chose this approach because Akaike's Information Criterion (AIC; Burnham and Anderson 1998) cannot be used with GEEs to select the optimal set of explanatory variables, and simulations suggest that the alternative quasi-likelihood under the independence model information criterion (QIC; Pan 2001) is also unreliable for GEEs (Barnett et al. 2010). For final models, we assessed goodness of fit using a marginal  $R^2$  for GEEs (Zheng 2000, Bailey et al. 2013) and receiver operating characteristic (ROC) scores for evaluating the classification accuracy of the models.

To estimate the geographic extent of the distribution of visitors at different levels of certainty, we produced seasonal probability surfaces by generating a grid of points each separated by 1 km in a 100-km buffer surrounding the calving grounds, calculating the sex-, season-, and herd-specific probability of being a visitor at each point from our

final GEE models, and rasterizing the grid of probability values. We trimmed the probability surfaces to the coastline wherever they extended over the ocean and calculated the magnitude of their areas (predicted area used by visitors/area of the calving grounds) at probability intervals of 0.1.

#### **Variation in Home Range Size and Calving Ground Residency Time**

To develop a more comprehensive understanding of the movement patterns responsible for differences in the seasonal probability values obtained from our final GEE models, we assessed variation in black bear home range size and the intensity of use of the calving grounds measured by calculating the amount of time bears spent in the calving grounds (hereafter, residency time). We estimated seasonal home range sizes for individual bears using 99% Brownian bridge utilization distribution kernels (Horne et al. 2007) and tested for differences between sex and herd in each season using linear mixed-effects models. We  $\log_{10}$ -transformed home range sizes to normalize and homogenize error variances for all analyses. We estimated the seasonal residency time of individual bears by calculating the percentage of locations that were within the borders of the calving grounds in each season, and tested for differences between sex and herd separately for visitors and non-visitors in each season using linear mixed-effects models.

To test for a population-level, aggregative response, we compared the herd-specific residency time of visitors during the calving season to all other seasons using linear mixed-effects models. We used the calving season as the intercept;

thus, a negative and statistically significant coefficient for other seasons would indicate that visitors decreased their residency times during those seasons in comparison with the calving season. We compared the herd-specific residency time of non-visitors during the calving season to all other seasons using linear mixed-effects models, again using the calving season as the intercept. For all linear mixed-effects models, we used restricted maximum likelihood (REML) to estimate fixed effects parameters, Satterthwaite's approximation to calculate *P*-values, and individual bear as the random effect. We conducted all analyses in program R version 3.0.2 (R Development Core Team 2013), relying on the packages *adehabitatHR* (Calenge 2006), *rgdal* (Keitt et al. 2013), *rgeos* (Bivand and Rundel 2013), *sp* (Bivand et al. 2008), *raster* (Hijmans and van Etten 2012), and *spatstat* (Baddeley and Turner 2005) for spatial analyses, *geopack* (Halekoh et al. 2006) to implement GEEs, *lme4* (Bates et al. 2013) to implement linear mixed-effects models, *lmerTest* (Kuznetsova et al. 2013) to calculate *P*-values for linear mixed-effects models, and *ROCR* (Sing et al. 2005) to calculate ROC scores.

## RESULTS

We had multiple years of calving season data for 18 black bears, and observed interannual fidelity to calving ground visitation patterns for 16 (89%) of these bears in 26 of 28 bear-years (93%; Supplemental Material Table S2). Bears that were classified as non-visitors (6 F, 3 M) in their first year of monitoring repeated this visitation pattern in succeeding years. Bears that were classified as visitors (3 F, 6 M) in their first year of monitoring repeated this visitation pattern in succeeding years, with 2 exceptions. In Middle Ridge, 2 male bears (both >4 years of age and monitored for 3 years) that were initially classified as visitors (1 in year 1, 1 in years 1 and 2), subsequently moved away from the calving grounds and became non-visitors.

Across all seasons, GEE model fit was good, and results showed that the predicted probability of a black bear being a visitor decreased as distance to the calving grounds increased (Figs. 2–3, Supplemental Material Table S3). Significant sex × distance interactions in all seasons indicated that the influence of distance to the calving grounds on the predicted probability of a bear being a visitor varied between males and females (all *P* < 0.033; Fig. 3, Supplemental Material Table S3). Regardless of season, probability curves derived from GEEs decayed more slowly for male bears than for female bears as distance increased, and the predicted probability of a male bear being a visitor was always greater than the predicted probability of a female bear being a visitor at distances beyond 2.4 km from the calving grounds (Fig. 3, Supplemental Material Table S3). During summer, there was a significant herd × distance interaction (*P* = 0.024; Supplemental Material Table S3); sex-specific predicted probabilities of being a visitor in the La Poile herd range were greater than corresponding sex-specific predicted probabilities of being a visitor in the Middle Ridge herd range at most distances (Fig. 3). The magnitude (predicted area used by visitors/area of the calving grounds) of the probability

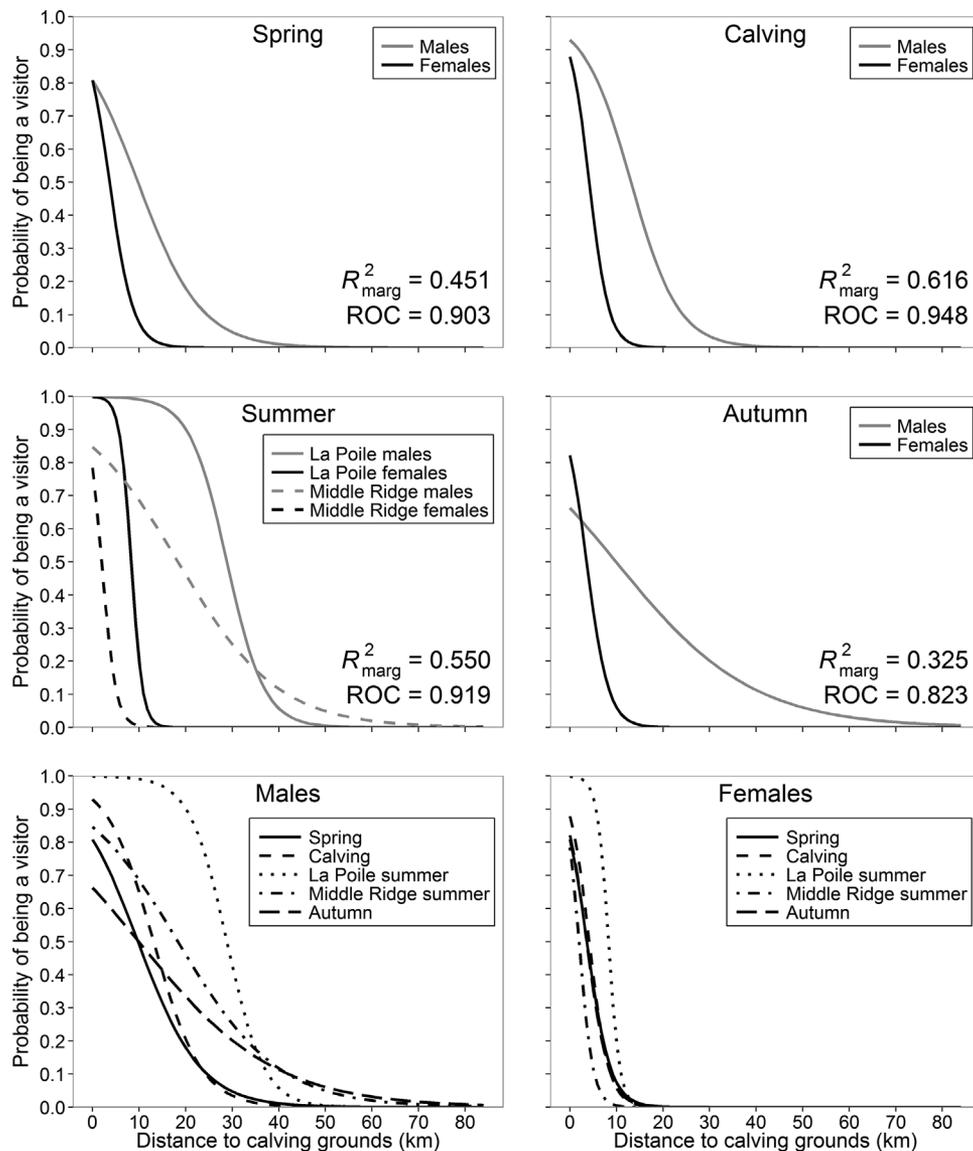
surfaces predicting the distribution of visitors was larger than the calving grounds in all seasons at all levels of certainty (Table 1, Supplemental Material Fig. S1). For example, the extent of the seasonal probability surfaces that encompassed the areas where bears had a ≥0.5 probability of visiting the calving grounds during the calving season in La Poile was 2.73–7.55 times larger than the calving grounds for male bears and 1.58–2.21 times larger for female bears (Table 1, Supplemental Material Fig. S1).

Male home ranges were 2.39–5.43 times larger than female home ranges in all seasons (all *P* < 0.001; Fig. 4A, Supplemental Material Table S4), but we detected no differences between herds (all *P* > 0.092). Evidence for increased intensity of use of the calving grounds during the calving season was equivocal; in La Poile, visitor residency time on the calving areas was an average of 2.02–5.29 times greater during calving than during all other seasons (all *P* < 0.02; Fig. 4B, Supplemental Material Table S5), suggesting an aggregative response. However, in Middle Ridge, visitor residency time was 0.27 times less during calving than during autumn (*P* = 0.040; Supplemental Material Table S5), but we detected no differences between calving and other seasons (both *P* > 0.240; Fig. 4B, Supplemental Material Table S5). During summer and autumn, visitor residency time was 4.99–5.36 times lower in La Poile than in Middle Ridge (both *P* < 0.006; Fig. 4B, Supplemental Material Table S5). Non-visitor residency time in Middle Ridge was 15.86–15.91 times greater during summer and autumn than during calving (both *P* < 0.035; Fig. 4B, Supplemental Material Table S5).

## DISCUSSION

We developed a simple but effective approach for identifying the relevant scale of predator-prey interactions and the distribution of potential predators in systems where aggregated prey species are exploited by non-obligate predators. Our research demonstrated that in systems with predictable, ephemeral, and concentrated distributions of cervid neonates, prey accessibility may be influenced by the broad-scale distribution and sex of predators. Our work also revealed that some black bears from our focal populations likely contributed to caribou calf mortality, whereas others likely did not. Parsing landscape-level spatial patterns of ursid-ungulate calf interactions may be especially important; neonate mortality caused by bears may play a key role in ungulate population dynamics and frequently appears to be additive because bears kill most neonates before body condition begins to mediate vulnerability to predation (Zager and Beecham 2006, Barber-Meyer et al. 2008, Griffin et al. 2011).

Our modeling framework allowed us to predict the probability that a black bear was potentially a calf predator based upon its sex, the herd range it occupied, its distance to the calving grounds, and the season in 2 caribou herd ranges in Newfoundland. Not surprisingly, in all seasons the probability that a bear was a visitor decreased with increasing distance from the calving grounds (Fig. 3, Supplemental Material Fig. S1). However, especially for male bears, the



**Figure 3.** Predicted seasonal probabilities of a black bear being within the calving grounds of the La Poile or Middle Ridge caribou herd >17% of the calving season (i.e., being a visitor) as a function of distance to the calving grounds (km), sex, and herd, estimated from generalized estimating equations (GEEs), Newfoundland, Canada, 2008–2013. Marginal  $R^2$  ( $R^2_{\text{marg}}$ ) and receiver operating characteristic (ROC) scores are provided for each GEE model.

predictive ability of our models and the probability of being a visitor at any given location varied seasonally (Fig. 3, Table 1). Additionally, patterns of residency time also varied among seasons, most notably for visitors in La Poile, which were rarely found inside the calving grounds after the calving season. Similarly, non-visitors in Middle Ridge increased their residency time in summer and fall (Fig. 4B, Supplemental Material Table S5). Thus, the extent of the area relevant to management actions (Table 1) and the certainty and efficacy with which those actions could target visitors (Figs. 3 and 4B) was dependent upon the caribou herd and the time of year. Overall, our results suggested that predator reduction would likely be most effective if it were carried out during the calving season and with a well-defined spatial extent. Additionally, our findings implied that predator reduction conducted in autumn, the most common season for black bear hunts in most jurisdictions, was least

likely to discriminate between visitors and non-visitors (Fig. 3). Although these findings may seem obvious, few studies have quantified the spatiotemporal distribution of potential calf predators, and failure to do so may have limited the efficacy of conservation efforts elsewhere. For example, Mosnier et al. (2008) examined the movements of coyotes and black bears in and around Gaspésie National Park, Quebec, Canada after 2 periods of predator control designed to improve calf survival of endangered Gaspésie caribou. They found that predator removals were carried out at a relatively local scale compared to the spatial extent of predator movements, likely lessening the effectiveness of the predator removals.

Although conspecifics within a population have frequently been considered to be ecologically equivalent, intrapopulation behavioral variation may exist (Bolnick et al. 2003). This variation may arise from individual specialization, sexual

**Table 1.** Magnitude (predicted area used by visitors/area of the calving grounds) of the predicted seasonal probability surfaces for male (M) and female (F) black bears based on the probability that the bear will be within the calving grounds of the La Poile or Middle Ridge caribou herd >17% of the calving season (i.e., be a visitor), Newfoundland, Canada, 2008–2013.

Herd	Probability of being a visitor	Spring		Calving		Summer		Autumn	
		M	F	M	F	M	F	M	F
La Poile (889 km <sup>2</sup> )	≥0.9			1.37		4.09	1.48		
	≥0.8	1.21	1.06	2.05	1.23	5.37	1.74		1.04
	≥0.7	1.76	1.28	2.55	1.41	6.28	1.92		1.26
	≥0.6	2.25	1.46	2.96	1.56	6.99	2.07	1.84	1.43
	≥0.5	2.73	1.62	3.32	1.69	7.55	2.21	2.88	1.58
	≥0.4	3.19	1.79	3.70	1.84	8.03	2.36	3.92	1.74
	≥0.3	3.70	1.98	4.12	2.00	8.52	2.52	5.16	1.93
	≥0.2	4.35	2.22	4.65	2.20	9.10	2.72	6.76	2.15
	≥0.1	5.40	2.59	5.49	2.50	9.98	3.00	8.56	2.51
Middle Ridge (1,456 km <sup>2</sup> )	≥0.9			1.32					
	≥0.8	1.17	1.05	1.97	1.19	1.80			1.03
	≥0.7	1.70	1.24	2.45	1.36	2.55	1.14		1.22
	≥0.6	2.17	1.41	2.88	1.50	3.23	1.27	1.77	1.38
	≥0.5	2.63	1.57	3.28	1.63	3.88	1.39	2.79	1.53
	≥0.4	3.14	1.72	3.69	1.77	4.57	1.51	3.94	1.68
	≥0.3	3.70	1.90	4.16	1.92	5.39	1.65	5.34	1.85
	≥0.2	4.42	2.13	4.76	2.11	6.44	1.82	7.25	2.07
	≥0.1	5.62	2.49	5.73	2.41	8.09	2.08	10.21	2.41

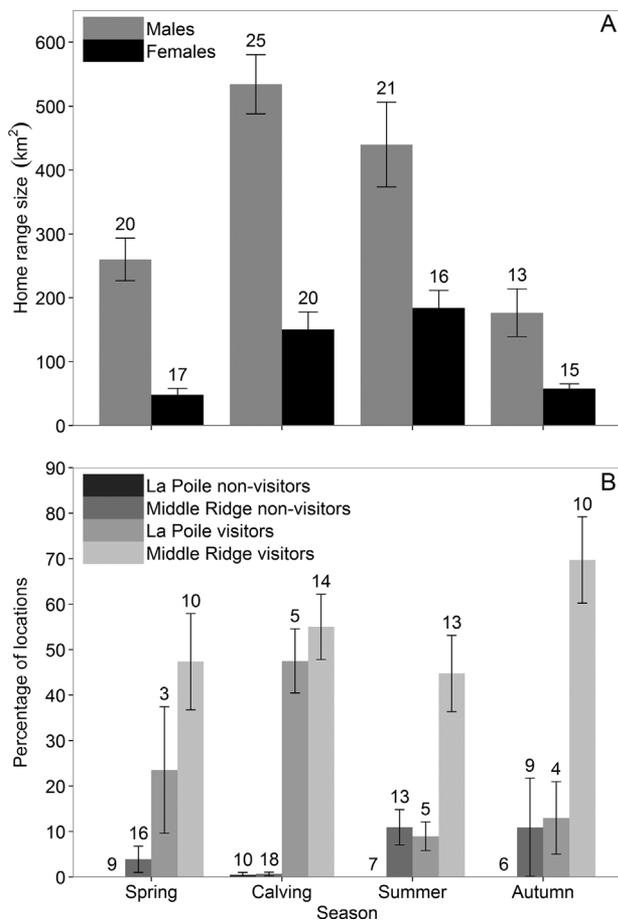
dimorphism, and ontogenetic niche shifts (Bolnick et al. 2003), or, because temporal and geographic heterogeneity in the distribution of resources and consumers restricts the foraging choices of some individuals (Angerbjörn et al. 1994, Ben-David et al. 1997). In our study, a bear's presence or absence inside the calving grounds during calving accurately predicted that bear's presence or absence inside the calving grounds during future calving seasons, with few exceptions (2 of 18 bears [11%], 2 of 28 bear-years [7%], Supplemental Material Table S2), demonstrating the possibility of interannual fidelity to seasonally predatory behavior.

Although research examining variation in consumer responses to pulsed resources has typically focused on interspecific differences (Wilmers et al. 2003), our intraspecific results concur with findings from those studies that wide-ranging consumers may be able to more effectively exploit pulsed resources than less vagile consumers. Consistent with findings from elsewhere in black bear range (Pelton 2003), we found differences between the size of male and female black bear home ranges, with male home ranges much larger than female home ranges in all seasons (Fig. 4A, Supplemental Material Table S4). Because of this, there was a greater probability that male visitors would be located farther from the calving grounds than female visitors.

Predation of ungulates by bears may be a learned behavior (Zager and Beecham 2006), and research has shown that some black bear foraging behaviors are transmitted through social learning and rearing condition (Mazur and Seher 2008). Female bears would be the principal transmitters of learned predatory behavior if this was true (Stewart et al. 1985). Preliminary results have identified 10 female and 12 male bears (all from Middle Ridge) at caribou calf kill sites in Newfoundland (M. Mumma, University of Idaho, unpublished data), but additional research is needed to further

investigate the prevalence and transmission of predatory behavior within the population of visitors. It may be difficult to distinguish between male and female black bears using readily available management techniques such as increased hunter harvest (Obbard et al. 2008). To account for this, our GEE models could easily be corrected by the sex ratio of the reported black bear harvest by hunters in Newfoundland, where from 2008 to 2013, 71% of all bears harvested were males (G. Luther, Government of Newfoundland and Labrador Department of Environment and Conservation, unpublished data). An educational program in conjunction with the use of suspended baits could help train hunters to distinguish between male and female bears if managers wanted to alter the sex ratio of harvested bears.

We found support for a population-level aggregative response to the resource pulse of caribou calves by black bears only for the La Poile herd, where visitor residency times in the calving grounds were substantially greater during calving than in any other season (Fig. 4B; Supplemental Material Table S5). We suggest that the synchrony of caribou parturition and increased visitor residency time may indicate that bears were opportunistically responding to the presence of caribou neonates in the La Poile calving grounds, but recognize that such coincidence does not establish causality. Regardless, visitors in La Poile were inside the calving grounds infrequently in the summer and autumn, whereas visitors in Middle Ridge spent more time in the calving grounds during these seasons (both  $P < 0.006$ ; Fig. 4B; Supplemental Material Table S5). These seasonal disparities imply that the La Poile calving grounds provided substantial resources for bears only during calving (and possibly spring), whereas the calving grounds in Middle Ridge provided more consistent resources throughout the year. Differences may have existed because the La Poile calving grounds were



**Figure 4.** A) Estimated mean  $\pm$  standard error seasonal home range size ( $\text{km}^2$ ; 99% Brownian bridge utilization distribution kernels) of male and female black bears, Newfoundland, 2008–2013. B) Mean  $\pm$  standard error seasonal percentage of black bear locations within the calving grounds of the La Poile and Middle Ridge caribou herds ( $\text{km}^2$ ) for bears classified as visitors and non-visitors, Newfoundland, Canada, 2008–2013. Numbers above error bars in A and B indicate sample sizes. Note that the summation of seasonal sample sizes in panel B is larger than panel A because the classification (visitor or non-visitor) of 2 bears changed between years (see Results for more details).

higher in elevation, had a harsher climate, less soft mast, and less forest cover (N. Rayl, University of Massachusetts, unpublished data) than the Middle Ridge calving grounds.

Although we did not find population-level support for an aggregative response to the pulse of caribou calves in Middle Ridge, we observed movements of 1 adult male that suggested that a segment of the bear population in that herd range may have been responding to caribou neonates by migrating to the calving grounds (cf. Bastille-Rousseau et al. 2011). This bear spent  $>52\%$  of the calving season and  $<6\%$  of the spring, summer, and autumn seasons within the calving grounds, and his movement patterns were consistent with Dingle and Drake's (2007) conceptualization of migration as an individual-based process involving persistent, less tortuous, larger, and longer movements (Supplemental Material Fig. S2). Individual-level variation in foraging behavior oriented towards neonates has been demonstrated in other ursid-ungulate systems, consistent with a continuum of individual specialization across a range of taxa (Bolnick et al. 2003). Whether or not this bear was

actively searching for caribou calves, or was simply taking advantage of opportunistic encounters (Bastille-Rousseau et al. 2011), his long-distance linear movements suggested selection for areas of high caribou calf density, though it is possible they were a result of breeding season movements.

## MANAGEMENT IMPLICATIONS

Wildlife managers seeking to reduce predation on depressed ungulate populations often contemplate reducing predator populations. Our findings suggest that if predator reductions are implemented in Newfoundland in an attempt to increase caribou calf survival, they would be most effective if focused during the calving season. Further, our results indicate that the spatial extent of predator reductions likely needs to be significantly larger than the area over which managers wish to increase calf survival. Although many agencies may have neither the resources nor time to evaluate the spatial structure of predator and prey populations prior to implementing predator reductions, it may be difficult to otherwise determine the most appropriate spatial scale of predator reductions. One plausible approach would be to experimentally manipulate predator densities at gradually increasing scales during the calving season.

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