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Spatial ecology of black bear (*Ursus americanus*), coyote (*Canis latrans*) and lynx (*Lynx canadensis*) in Newfoundland

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Newfoundland Caribou Strategy

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Environment and Conservation

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EXECUTIVE SUMMARY

To understand and address the challenge of Newfoundland's declining caribou population, the Government of Newfoundland and Labrador implemented a five-year *Caribou Strategy* for the island, beginning in 2008. The *Caribou Strategy* is a comprehensive research and management program to improve ecosystem-level knowledge of caribou and their predators, and test means to mitigate predation mortality on calves. Research to date suggests the demographic mechanism underlying the population decline is high levels of calf mortality due to predation, primarily by black bear (*Ursus americanus*), and coyote (*Canis latrans*), and to a lesser extent lynx (*Lynx canadensis*) and Bald Eagle (*Haliaeetus leucocephalus*).

Knowledge of predator ecology is therefore critical to developing integrated management approaches for caribou and predators. Predator space use is a fundamental aspect of predator ecology that strongly influences their population dynamics and their use of prey. The size and location of predator home ranges and the consistency of space use over time are important determinants of predator encounter rates with caribou. Likewise, the rate of predator movement across the landscape also influences predator interactions with prey, and also the ability of predators to occupy new territories or recolonize areas where removal or extirpation has taken place. Additionally, changes in predator space use may precede observations of demographic or habitat changes and may thereby function as an early warning of such changes. Despite these important ecosystem relationships there has been minimal work on predator spatial ecology in Newfoundland.

This study was conducted using data amassed from the *Caribou Strategy* between 2008 and 2013. Radio-telemetry tracking of 88 black bears, 79 coyote, and 13 lynx was employed to investigate predator home range size, site fidelity, and daily movement rate. Patterns in these spatial quantities were elucidated in relation to season, study area, sex, and predator behavioral mode (resident or transient, for coyotes only). The most important findings include:

Home range size
- Coyotes displayed two distinct behavior modes: resident coyotes occupied defined home ranges for prolonged periods while transient coyotes made large-scale movements, roaming widely between regions of the island.

- Home ranges for all species were notably large in comparison with populations in most other areas of North America.

- Male black bear home ranges were larger than those of females, and transient coyote home ranges were almost five times larger than those for resident coyotes.

- Black bear spring and summer home ranges were larger than those in fall and winter, while coyote spring home ranges were smallest and winter ranges largest.

Site fidelity
- Most animals, with the notable exception of transient coyotes, were relatively consistent in their location from one year to the next. For any given date, animals were likely to be found, on average, within 12 km of their position on the same date in the previous year,

although the exact distance varied by species, season, and study area.

- Females displayed greater site fidelity than males for both bears and resident coyotes.

Daily movement rate
- Extreme long-distance movements of transient coyotes enabled them to cross the island of Newfoundland in a few weeks, suggesting a well-developed capacity to colonize new areas or recolonize areas depleted by management action. However, the daily movement rate (i.e. kilometers traveled per day) was not as drastically different between resident and transient coyotes as the difference in their home range sizes might suggest. This indicates that the much larger home ranges of transient coyotes were the result of *where* they chose to go and not because transient coyotes travelled further each day in comparison to resident coyotes.

- Black bear movement rates were greatest in spring when food was likely less abundant than in other seasons, and movement rates for male black bears exceeded those for females, particularly during spring, when male black bears search widely for multiple mates.

- In contrast to other regions of North America, male resident coyotes in Newfoundland had greater daily movement rates than females, for unknown reasons.

- Lynx had greater daily movement rates in spring while other seasons were similar.

This study has illuminated patterns in the basic spatial ecology of caribou predators in insular Newfoundland. One of the most significant findings relative to predator management is the long distance movement of transient coyotes. The ability of this canid to cross Newfoundland in a few weeks suggests that any area depopulated by directed management action such as predator removal, could be quickly re-colonized. In addition, the home range size of bears and coyotes in this study are amongst the largest reported in North America. Such large home ranges increase the likelihood of home range overlap between caribou and predators, although the low density of predators may reduce the likelihood of encounter.

This study has been the first to outline patterns of predator space use in relation to a number of fundamental variables (i.e. sex, season, study area, and behavior mode) and provides a foundation to inform our understanding of both their observed predation on caribou and implications and utility of predator management strategies.

Table of Contents

List of Tables

List of Figures

INTRODUCTION

Woodland caribou (*Rangifer tarandus caribou*) are listed as "At Risk" throughout North America under the Canadian Species At Risk Act and the US Endangered Species Act, with the exception of the Newfoundland population. Newfoundland's caribou population has declined from approximately 94,000 animals in the mid-1990s to *ca.* 33,000 in 2013, and Newfoundland caribou may become listed as "At-Risk" by 2014 (Randell et al. 2012, Weir et al. 2013). To address the declining caribou population, the Government of Newfoundland and Labrador implemented a five-year *Caribou Strategy* for the island, beginning in 2008. The *Caribou Strategy* is a comprehensive research and management program to improve ecosystem-level knowledge of caribou and their predators and test means to mitigate predation mortality on calves. Research to date suggests the demographic mechanism underlying the population decline is high levels of calf mortality due to predation by black bear (*Ursus americanus*), coyote (*Canis latrans*), lynx (*Lynx canadensis*), and bald eagle (*Haliaeetus leucocephalus*) (Trindade et al. 2011).

On account of the important role played by predators in the caribou population decline, an integral component of the *Caribou Strategy* is to examine the relationship between predators and caribou. The numerical, functional, and behavioural responses of predators vary with the population dynamics of prey (O'Donoghue et al. 1997, 1998a, 1998b), the overlap in habitat use (Brown et al. 1999), and the feeding strategy of the predator (Ryall and Fahrig 2006). In turn, the presence or absence of predators strongly influences the behaviour, population, and space-use dynamics of prey (Lima and Dill 1990).

However, predator ecology is not only important theoretically but also for management of predators and prey. Predator ecology has been increasingly studied as one aspect of predator control efforts (e.g., Landriault et al. 2009), but the lack of information on predators is often a major weakness in predator control programs (National Research Council 1997). Predator studies have been conducted in Newfoundland (Bergerud 1983, Mahoney 1991, Day 1997, Mahoney et al. 1997, McGrath et al. 2009), but these were generally single-species focused programs and not considered in the context of prey ecology. There remains a deficiency in our basic knowledge of predator ecology and predator–prey relationships that must be redressed to effectively manage predators and prey and to control predators if necessary.

A critical aspect of predator ecology for management and ecological understanding is space use. Predator space use is a fundamental quantity with obvious implications for spatial and temporal interactions between caribou and their predators. For example, the extent to which predators occupy territories, as opposed to leading a nomadic existence, and the location and seasonality of home ranges is an important determinant of predator overlap in space and time with caribou (Rayl 2012). Home range size varies with the availability of food (Gomper and Gittleman 1991, Patterson and Messier 2001, Dobey et al. 2005, Young et al. 2008) and is an important determinant of the extent of overlap with caribou ranges (particularly with respect to caribou calving areas). Likewise, the consistency of individual predator space use over time (i.e., site fidelity) is an important indicator of the predictability of food abundance (Wiens 1976, Switzer 1993, Murray et al. 1994, Gende and Quinn 2004, Wittmer et al. 2006), and predator site fidelity is known to increase as predator density reaches habitat saturation (Kitchen et al. 2000). Knowledge of predator site fidelity is crucial for predator management, particularly in guiding the spatial scale of predator removals (Sacks et al. 1999). Predator movement across the landscape is also of fundamental importance, since it determines interactions with prey (Garneau

et al. 2008, Bastille-Rousseau et al. 2011, Rayl 2012) and the rate at which predators disperse to occupy new territories (Hinton et al 2012) or recolonize areas where removal or extirpation has taken place (Benson and Chamberlain 2007). Home range size, scale of movements across the island, and levels of site fidelity will all influence the long-term utility of any predator management efforts.

To date, caribou mammalian predator (black bear, coyote, and lynx) spatial ecology in Newfoundland has received relatively little attention. Coyotes are known to have large home ranges on the island (McGrath et al. 2009), and their seasonal use of space indicates that they are adapting to local food conditions, exploiting the most abundant food at a local scale and not making major seasonal shifts to congregate in known caribou areas (McCue 2012).

This study was conducted with data amassed between 2008 and 2013. The objective was to provide a foundational descriptive understanding of caribou predator home range sizes, site fidelity, and movement rates in relation to factors that affect these quantities including sex, season, and study area. As such, it is an exploratory analysis that necessarily forms the basis upon which ecological hypotheses of predator–prey interaction can be tested, and upon which predator management can be based.

METHODS

Study Species

Black bears are the largest native Newfoundland predator and are capable of individually killing adult caribou. They have been well studied (including their spatial ecology) in other regions of North America (e.g., Rogers 1987, Benson and Chamberlain 2007, Mitchell and Powell 2007, Costello et al. 2008, Garneau et al. 2008, Noyce and Garshelis 2011). In Newfoundland previous to the *Caribou Strategy*, bear ecology research has been conducted in Gros Morne National Park (Day 1997, Mahoney et al. 1997), around Serpentine Lake (Dennis et al. 1996), and in the Northwest Gander River area (Mahoney 1991). This is the first study to focus specifically on spatial ecology and the first to use GPS collars on bears in Newfoundland.

Coyotes have rapidly expanded their range across North America and their colonization success may be due in part to their tremendous ability to traverse long distances and establish home ranges in novel landscapes (Hinton et al. 2012). Coyotes have recently colonized the island of Newfoundland and since arriving have established themselves as an important component of caribou predation (particularly neonates; Mahoney and Weir 2009, Trindade et al. 2011), although it is not clear whether coyote predation is additive (i.e., in addition to that by other predators) or compensatory (i.e., taking animals that other predators would have killed anyway).

Lynx, as specialist predators, are assumed to be largely restricted to the same habitat as their primary prey, snowshoe hare (*Lepus americanus*) (Ryall and Fahrig 2006). Nonetheless, numerous cases of long distance (> 100 km) dispersal movements have been documented, indicating that lynx have some flexibility in habitat selection (Ward and Krebs 1985, Slough and Mowat 1996, O'Donoghue et al. 1997, Poole 1997). When hare numbers decline, lynx productivity declines, while movements, home range, and mortality increase (Brand et al. 1976, Ward and Krebs 1985, Poole 1994, O'Donoghue et al. 1997). However, prey switching to caribou calves previously positioned lynx as the primary predator of these animals (Bergerud 1983), but recent studies suggest that this is no longer the case (Mahoney and Weir 2009, Trindade et al. 2011, Lewis et al. 2013).

Study Areas

Ecological research for the *Caribou Strategy* is conducted mainly in three study areas: Middle Ridge, La Poile, and the Northern Peninsula (Figure 1). These areas were selected using the following caribou-specific criteria: 1) geographic separation among study areas, 2) an abundance of existing information on Middle Ridge and La Poile, 3) the paucity of data for Northern Peninsula caribou in conjunction with the known ecological separation of these caribou from the rest of the island herds (to confirm whether population trends are island-wide or regional), and 4) the caribou herds that occupy these regions represent approximately 50% of the island population.
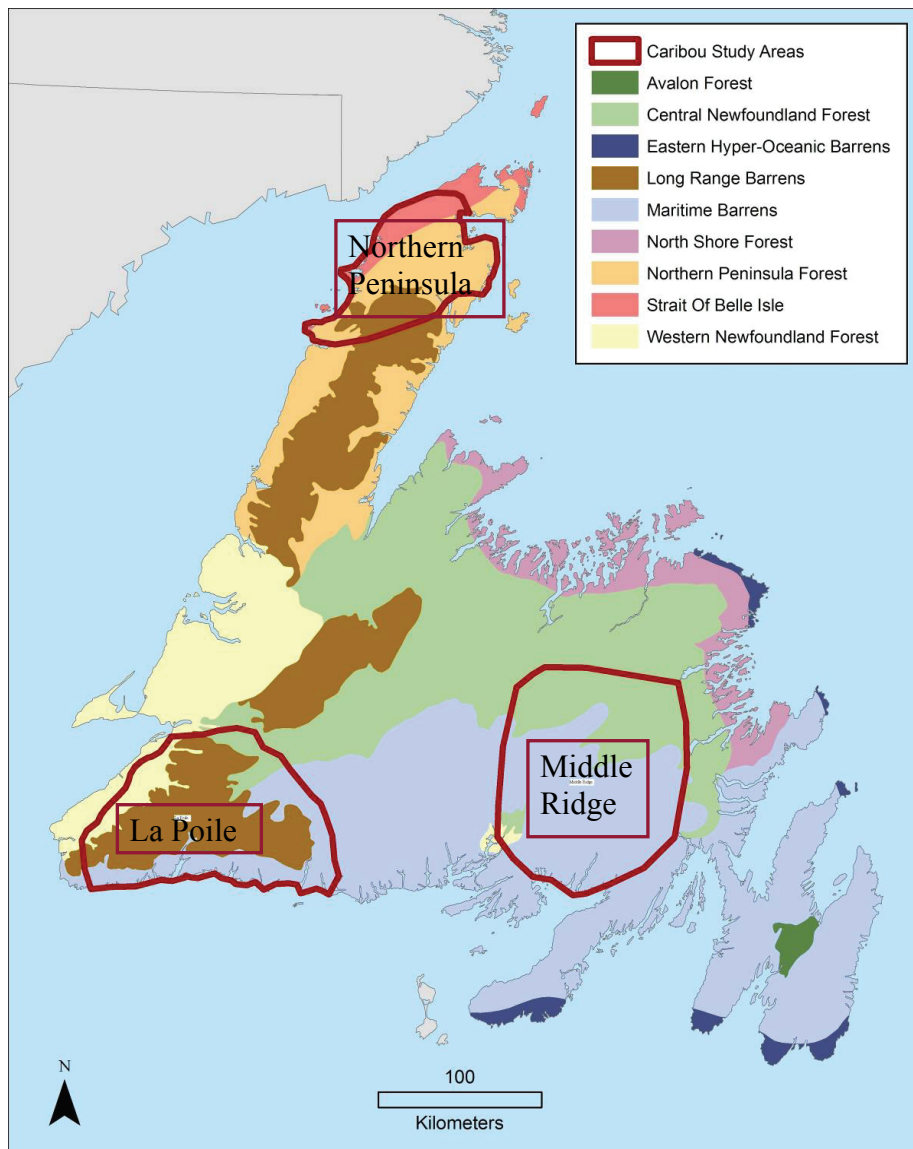
Figure 1. The ecoregions of Newfoundland and the *Caribou Strategy* study areas during 2008–2013: Middle Ridge in the east, La Poile in the west, and the Northern Peninsula in the north.

Middle Ridge

The Middle Ridge study area (13,369 km^2) is located in the interior of eastern/central Newfoundland, encompassing the Bay du Nord Wilderness Area and the Middle Ridge Wildlife Reserve that cover 22% and 4.5% of the total study area, respectively (see Fifield and Lewis 2013, p. 3). Bogs are prevalent throughout this region and balsam fir (*Abies balsamea*) is the dominant tree species in forested areas. This study area has two main calving areas; the northern calving ground overlaps the Central Newfoundland Forest Ecoregion and the Maritime Barrens Ecoregion, while the southern calving ground is entirely within the latter. In addition to the two main calving areas, some calves are born to the east of the northern calving ground in the Meta Pond area.

Forest fires have been historically common in much of the Middle Ridge area, altering the successional trajectory from balsam fir to black spruce (*Picea mariana*) and sometimes birch (*Betula* spp.) to aspen (*Populus* spp.) (Meades 1990). The disturbance history of Middle Ridge also includes widespread insect outbreaks (i.e., hemlock looper (*Lambdina fiscellaria*) and spruce budworm (*Choristoneura fumiferana*)). Among the study areas, human disturbance is probably lowest in Middle Ridge. The Bay d'Espoir Highway runs through the western portion of Middle Ridge but the only communities are in the Conne River and Pool's Cove areas to the southwest and English Harbor East in the southeast of the study area. Logging roads are prevalent off the highway, especially in the northwestern section. Disturbance is minimal in southern Middle Ridge.

La Poile

The La Poile study area (11,251 km^2) overlaps three ecoregions: the Long Range Mountains Ecoregion, the Western Newfoundland Forest Ecoregion, and the Maritime Barrens Ecoregion (Figure 1). The Long Range Mountains Ecoregion is mostly covered by heath and moss barrens, rock outcrops, with some sparse forest patches. West of that ecoregion is a small band of the Western Newfoundland Forest Ecoregion, characterized by balsam fir forest with black spruce and larch (*Larix laricina*) on the wetter sites (Meades 1990). Forestry has been prevalent in this ecoregion, but since caribou are generally found to the west of this ecoregion, influence is likely minimal. Roads border La Poile to the west, north, and east while the area extends to the coastline in the south. Logging roads are extensive in the northern areas but communities are few. Human disturbance is minimal in the south.

The Northern Peninsula

The Northern Peninsula study area (5,711 km^2) overlaps three ecoregions: the Strait of Belle Isle, the Northern Peninsula Forest, and the Long Range Barrens (Figure 1). The Strait of Belle Isle Ecoregion is on the northern tip of the peninsula and is characterized by an abundance of wetlands, particularly lowlands of sloping bog plateaus. The Northern Peninsula Forest Ecoregion is on the eastern side of the highlands and is primarily composed of balsam fir and black spruce forest. Limestone barrens are common along the west coast, with dwarf shrub and crowberry (*Empetrum* spp.) barrens on the east coast. The Long Range Barrens Ecoregion includes the highlands of the Long Range Mountains, above the treeline. The trees of this ecoregion are mostly windswept spruce and larch (i.e., krummholz, locally known as "tuckamore"). The vegetation is primarily that of alpine barren, dominated by arctic-alpine plants

or crowberry barren. Fens and bogs also cover much of this ecoregion (Meades 1990). Human disturbance is probably greatest in this study area including relatively extensive forest harvesting in comparison with the other study areas. Highways border the western side of the study area and smaller roads run east–west across the Northern Peninsula. There are a number of communities in the study area.

Capture Methods

In all three study areas, predators were captured by live-trapping or by netting or darting from a helicopter. Trapping on the ground was emphasized in La Poile and the Northern Peninsula for both bears and coyotes because of good road access into those areas. Middle Ridge has few secondary roads that were suitable for ground trapping, so capture with a helicopter predominated there. Bears were trapped using Aldrich-type spring-activated foot snares, whereas coyotes were trapped with #3 Oneida Victor Soft Catch traps (Oneida Victor Inc. Ltd., Euclid, Ohio). In 2008, lynx were trapped using #3 Oneida Victor Soft Catch traps, but because of poor trapping success and the desire to transition to a more ethical approach for winter trapping, box traps were used in 2009–2011 (Kolbe et al. 2003). From helicopters, tranquilizing darts were used for bears, while net guns (CODA Enterprises, Mesa, Ariz.) were used to capture coyotes.

Handling and Collaring

All animals were immobilized using Telazol (a combination of tiletamine and zolazepam) either by dart gun (bears) or by hand injection while being manually restrained (coyotes and lynx). Dosages (based on estimated weight) were 5 mg·kg^{-1} for bears, 10 mg·kg^{-1} for coyotes, and 5–10 mg·kg^{-1}, depending upon environmental conditions (e.g., less in extreme cold), for lynx. After immobilization, animals were periodically monitored for changes in vital signs, temperature, pulse rate, and respiration rate.

Black bear

Bears were fitted with one of three GPS collar types. Lotek GPS4400M remotely downloadable, mortality-sensing collars (1250 g, Lotek Wireless Inc., Newmarket, Ont.) were used in 2008–2011 to record locations for two years with a projected battery life of 2.5 years. Fix intervals varied throughout the year: 2 hours during the calving season (21 May – 31 July), 4 hours during the non-calving season (1 August – 31 December and 1 April – 20 May), and 12 hours during the winter (1 January – 31 March). These collars had timed release mechanisms that activated two years after initial deployment. IridiumTrackM 3D collars (1600 g, Lotek Wireless Inc.) were used in 2011 and had the same fix rate as the 4400M. Unfortunately these collars, which were a new prototype and supposed to have a two-year field life, did not last as long as expected. Most of the collars ceased to function during the denning period because of a design flaw that caused the collar's battery to be drained prematurely. This loss of collars resulted in far fewer bears collared for much shorter periods of time than was initially hoped. Advanced Telemetry Systems Iridium G2110E collars were deployed in 2012 with a similar fix rate.

Coyote

Coyotes were fitted with remotely downloadable, mortality-sensing collars (500 g, Telemetry Solutions custom design based on Quantum 5000 GPS collars, Concord, Calif.) in 2008–2010. Lotek GPS7000SA GPS/ARGOS collars (420 g, Lotek Wireless Inc.) were deployed in 2010–2013. All collars were programmed to record locations for the duration of the two-year battery life. Fix intervals were between 3–4 hours from 21 May to 31 July and 5–8 hours the remainder of the year depending on the collar type. There were no drop-offs on these collars because of the increased weight that could adversely affect coyotes.

Lynx

GWC181 GPS Store-on-board collars (280 g, SirTrack Ltd., Havelock North, New Zealand) were deployed in 2009, along with SirTrack AGC181 ARGOS collars (295 g) in 2010. In 2011 and 2012, Tellus 1C Light Lynx Collar/GPS Remote Download (220 g, Followit, Sweden via Zoha Ecoworks, Calgary) were used. The SirTrack GPS collars took a fix every 5 hours, the Tellus collars every 4 hours, and the ARGOS transmitted for 6 hours every third day.

Data Preparation

Data were downloaded from collars and stored in a Microsoft Access database. Some collars provided information on position accuracy but this varied by collar type within and among species. When GPS fix accuracy was available, it was categorized as 3-D (fix accurate in three dimensions, i.e., location and altitude), 2-D (fix location accurate, but not altitude), and No (fix inaccurate). For bears, 2-D fixes with dilution of precision (DOP) > 5 were discarded. For coyotes, all 3-D and 2-D fixes were retained (DOP information not available). For lynx GPS fixes, all 3-D, 2-D fixes, and fixes with no 2-D/3-D information were retained. Lynx ARGOS fixes with location classes 1, 2, or 3 were retained.

Analyses

Coyote behaviour mode

Some coyotes displayed territorial behaviour while others wandered widely. Coyotes were therefore classified as either "resident" or "transient" to better understand the effect of these behaviour modes on home range size, site fidelity, and daily movement rates. Each animal was classified based on the maximum distance between any two of its locations. The histogram of these distances was plotted and all animals with distances greater than the 75th percentile were classified as transients. The choice of the 75th percentile gave good correspondence to a subjective assignment based on visual inspection of mapped locations. This resulted in 15 coyotes classed as transients (13 males, 2 females). Two animals (1 male, 1 female) classed as residents by this approach had annual home range areas exceeding all other resident coyotes by more than five standard deviations and were removed from the analysis.

Attempts to use other movement metrics to differentiate these behaviour modes included the straightness index (Batschelet 1981), first passage time (Fauchald and Tveraa 2003), sum of the square displacement (scaled by either path length or number of fixes), and the size of the 95% kernel home range (optionally scaled by path length). However, none of these metrics

provided a clear division between animals that maintained localized territories versus those that roamed widely across the province, highlighting the difficulty in making such an objective classification. Indeed, it may be that metrics based on emergent behaviour, such as site fidelity, offer better methods of defining territorial versus transient coyotes.

Home range size

We defined the term "home range" broadly to mean "any area traveled in search of food" (Burt 1943) in contrast with the concept of "territory" (any area that is actively defended). This definition allows for the discussion of home ranges for all our study species, including transient coyotes.

Fixed-kernel estimates were used to estimate predator home ranges. Kernel density estimation is a well-accepted probabilistic statistical approach (Worton 1989) that has been extensively used to visualize the intensity of animal space use from a sample of locations provided by tracking collars. Briefly, the kernel method converts animal locations into a utilization distribution (UD): a 3-D projection of the locations where high peaks correspond to areas of intense animal usage and valleys correspond to areas of lesser use. The intensity of space usage is directly proportional to the volume of the peaks that protrude through a horizontal plane in the density surface. As is common, home ranges were indicated by the 95% UD (area inscribed upon the landscape when 95% of the volume of the peaks protrudes through the plane) that includes all important areas but eliminates regions of very low use (Laver and Kelly 2008). UDs were calculated using the adehabitatHR package (Callenge 2006) in R 2.15.1 (R Core Team 2012) using a fixed Gaussian kernel estimator with a bandwidth and grid cell size of 1000 m.

Both annual and seasonal home ranges were calculated. Annual home ranges were calculated from any available consecutive 365-day period. Seasons were based on the *Caribou Data Synthesis* (Mahoney 2000) and are defined as spring (May and June), summer (July, August, and September), fall (October and November), and winter (December, January, February, March, and April) (Mahoney and Weir 2009). The seasons are based on the caribou annual cycle since the objective is to understand predator spatial ecology in relation to caribou life cycle. For home ranges to be representative of the period of interest (either annual or seasonal) and to maintain adequate sample sizes for analyses, coyotes and bears were required to have fixes spanning 80% of the date range of the period and fixes on 80% and 40% of the days during the period for coyotes and bears, respectively. The smaller percentage of days required for bears accounts for the winter denning period when relatively few fixes are obtained. For lynx, this was modified to fixes spanning 80% of the date range and fixes on 30% of the days, since the ARGOS collars worn by lynx only produced a fix every three days.

Site fidelity

Site fidelity was assessed by the distance between fixes from the same individual separated by one year (Schaefer et al. 2000) with a resolution of five days. Smaller distances imply greater site fidelity. Thus, for each animal, we calculated distances between any two fixes during a five-day period in one year and the corresponding five-day period in the subsequent year, beginning with the first calendar day of the year (Schaefer and Mahoney 2013). This helped to reduce serial autocorrelation between temporally adjacent fixes to a level that could be ameliorated with existing statistical modeling tools (see Statistical Modeling below). Multiple distance measurements for an individual during a given five-day period were averaged to maintain the

animal as the experimental unit. The date of the mean distance was taken as the first day of the five-day period.

Daily movement rate

Daily movement rate (i.e., speed in km·d^{-1}) was computed as the straight line distance between fixes on consecutive days for an individual. Distance moved (and thus speed) depends upon the temporal resolution of fixes. Taking fixes more often reveals the finer structure of the movement paths and increases the overall measured length. To equalize disparate fix rates between species and collars, we chose a single fix per day closest to noon local time (Schaefer and Mahoney 2013). Similar to the site fidelity analysis, movement rate was computed at a resolution of seven days to reduce serial autocorrelation between consecutive fixes sufficiently to allow any remaining autocorrelation to be accounted for using mixed effects models (see Statistical Modeling below). For each animal, the movement rate for each seven-day period (starting at the beginning of the calendar year) was calculated as the mean of all inter-day movement rates during that period. The date of this mean movement rate was taken to be that of the first day of the period.

Statistical modeling

Standard linear modeling theory requires that several assumptions be met to produce accurate and precise predictions. Ecological data sets rarely meet these assumptions and therefore standard linear models (i.e., linear regression, ANOVA, etc.) can produce biased predictions. For example, in our data set, independence (i.e., the assumption that each data point is independent of others) is violated by the fact that there are multiple home range size, site fidelity, or movement rate measures for most animals (e.g., multiple years of data) that are likely to be more similar to each other than they are to data points for another animal and are thus not independent. Likewise, homogeneity of variance (i.e., the assumption that the extent of variability in the data is consistent across levels of a categorical variable) is violated because the extent of variation in a measurement (i.e., home range, site fidelity, and daily movement rate) often differs between males and females or among study areas or seasons. Additionally, our data are unbalanced (i.e., there are often unequal numbers of data points among sexes, study areas, or seasons). Linear mixed effects models (LMMs; Pinheiro and Bates 2000) are an extension to standard linear models that include mathematical machinery to accommodate and ameliorate violations of these assumptions. LMMs as implemented in the R *nlme* package (Pinheiro et al. 2013) were therefore used for all analyses.

A similar modeling philosophy was employed for all analyses (home range size, site fidelity, and daily movement rate). For each analysis, the effects of sex, behaviour mode (resident vs. transient), study area, season, and as many interactions[1] as possible (limited by sample size) were investigated. Since almost all transient coyotes were males ($n = 13$ of 15), meaningful statistical comparisons of transient versus resident coyotes only included males. It

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[1] A statistical interaction occurs when the effect of one explanatory variable depends upon the value of another explanatory variable. For example, male black bears had larger annual home ranges than females but the extent of the difference in home range sizes varied significantly among study areas. If the extent of the difference in home range size had been similar across study areas, there would have been no significant statistical interaction.

was not possible to additionally include age class as an explanatory variable in the models because of a lack of sufficient known-age animals in each sex/study area/season combination. Individual animals were included as a random intercept where necessary (as judged by likelihood ratio tests between models with and without the random term; Zuur et al. 2009) to account for repeated samples from some individuals that would otherwise invalidate model assumptions and constitute pseudo-replication.

The assumption of normality of residuals was assessed by plotting histograms of residuals and normal quantile–quantile plots. Heterogeneity of variance was assessed by plots of residuals versus fitted values and residuals versus each model term. Excessive heterogeneity was ameliorated by including an appropriate weighting structure in the model to equalize residual spread (Zuur et al. 2009). The exact weighting structure employed depended upon the nature and extent of the heterogeneity in a given model, and competing weighting structures (and the necessity for any weighting structure at all) were judged by comparing the Akaike Information Criteria (AIC; Burnham and Anderson 2002) for each model.

The assumption of independence was tested with serial autocorrelation plots of model residuals. Excessive autocorrelation is another form of pseudo-replication that can artificially deflate standard errors and p-values and therefore drastically increase the probability of committing a Type I error (i.e., finding a significant effect of an explanatory variable when there is in fact none). It is particularly problematic for time series data such as those used for the site fidelity and daily movement rate analyses. Serial autocorrelation was mitigated by including a correlation structure in the model (Pinheiro and Bates 2000) in addition to averaging site fidelity and daily movement rates over a period of several days (see above). Various correlation structures are available (autoregressive, autoregressive moving average, linear, spherical, Gaussian, etc.), and the best structure was chosen by comparing the AIC values for competing models and through visual inspection of remaining residual autocorrelation after the inclusion of correlation structure in the model (Zuur et al. 2009).

The bear data included both adult and sub-adult males. Sub-adult males making dispersive movements can exhibit annual home ranges that are larger than those of adult males (LeCount 1980, Smith and Pelton 1990). If this were the case in our data set, bias would be introduced if these ages classes were lumped during analysis. Nonetheless, sample size was not large enough to split the data into adult and sub-adult males in the statistical models of interest. An exploratory analysis of known-age adult and sub-adult males ($n = 8$ and 6, respectively; aged by first premolar tooth section; Willey 1974) found no significant differences between these age classes for annual home range size, site fidelity, and daily movement rate ($p = 1.0$, 0.09, and 0.46, respectively). Therefore, we combined the data for all males into a single category ("male") for analysis. Assuming similar behaviour for the rest of the unaged males in the sample, pooling all the male bears should not significantly bias the results.

R code for the analyses is available upon request.

Comparisons with Previous Research

Direct comparisons of home ranges, site fidelity, and daily movement rates from previous studies are problematic because of differences in collar technology (VHF vs. ARGOS vs. GPS), data collection methods, definition of seasons, ages and sexes of animals involved, relative timing of population cycles, and computational techniques (e.g., minimum convex polygon, kernel UD, etc.) among studies (Laundré and Keller 1984, Poole 1994, 2003). For example, for bears in

particular, our sample of males included an unknown number of sub-adults that could make comparison with studies of adults (exclusively) difficult. However, an exploratory analysis of our known-age bears failed to find a significant difference in home range size between adult and sub-adult males. We make direct comparisons between this study and the published literature but these differences should be borne in mind when assessing comparisons of our results with previous studies.

Tables Versus Figures

There is a subtle yet important distinction between the information presented in the tables and plots in the Results section. Table cells present means (± SD) of the raw data. Since this data typically fails to meet modeling assumptions (i.e., lack of independence, homogeneity of variance, etc., see Statistical modeling above), these cell means (± SD) can only be considered a rough approximation of the true values of interest and are likely biased. However, the fitted values (i.e., predictions) from LMMs that are presented in the figures (± 95% CI) *are* unbiased estimates of these values.

RESULTS

Black Bear

Individual black bears (n = 88; 46 males, 42 females) were tracked during 2008–2013 for an average of 394 ± 323 (range: 1–1,281) days producing 183,013 positions (Figure 2, Table 1).
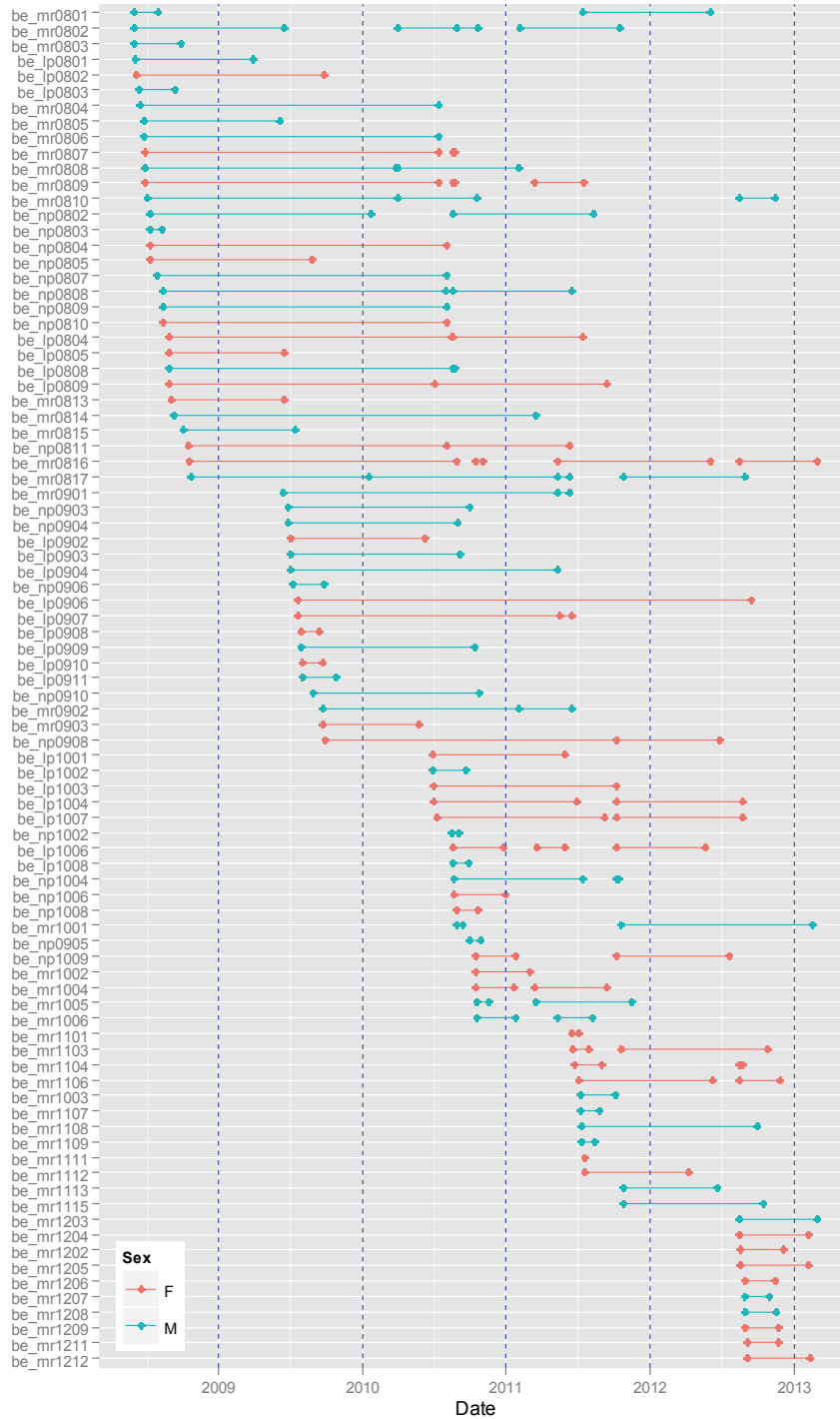
Figure 2. Duration of collaring and sex for 88 black bears (*Ursus americanus*) in Newfoundland, 2008–2013. Note continuous data were not always available between collar deployment and removal because of winter denning, battery depletion, or collar failure. LP = La Poile, MR = Middle Ridge, and NP = Northern Peninsula.

Table 1. Summary of black bear (*Ursus americanus*) telemetry data in Newfoundland during 2008–2013 showing number of animals collared, number of positional fixes obtained, and mean number of days monitored by study area and sex.

Study area	Sex	Number of animals	Number of fixes	Mean (± SD) monitoring days
La Poile	F	14	47,598	534 (345)
	M	9	11,636	271 (235)
	Total	23	59,234	431 (328)
Middle Ridge	F	20	33,454	288 (328)
	M	25	50,658	425 (321)
	Total	45	84,112	364 (328)
Northern Peninsula	F	8	21,413	535 (337)
	M	12	18,254	346 (291)
	Total	20	39,667	422 (317)
Sex totals	F	42	102,465	417 (350)
	M	46	80,548	374 (299)
Overall total		88	183,013	394 (323)

Home range size

Annual home range

Annual home range sizes ($n = 62$ for 41 animals, range: 54–1,347 km^2; Figure 3) varied greatly between sexes and, to a lesser extent, among study areas (Table 2, Figure 4). Males had larger home ranges than females in all study areas, but the extent of the difference varied among areas with the greatest difference in La Poile followed by Middle Ridge and the Northern Peninsula (significant interaction of sex with study area: $F_{2,35} = 4.41$, $p = 0.02$; Figure 4).
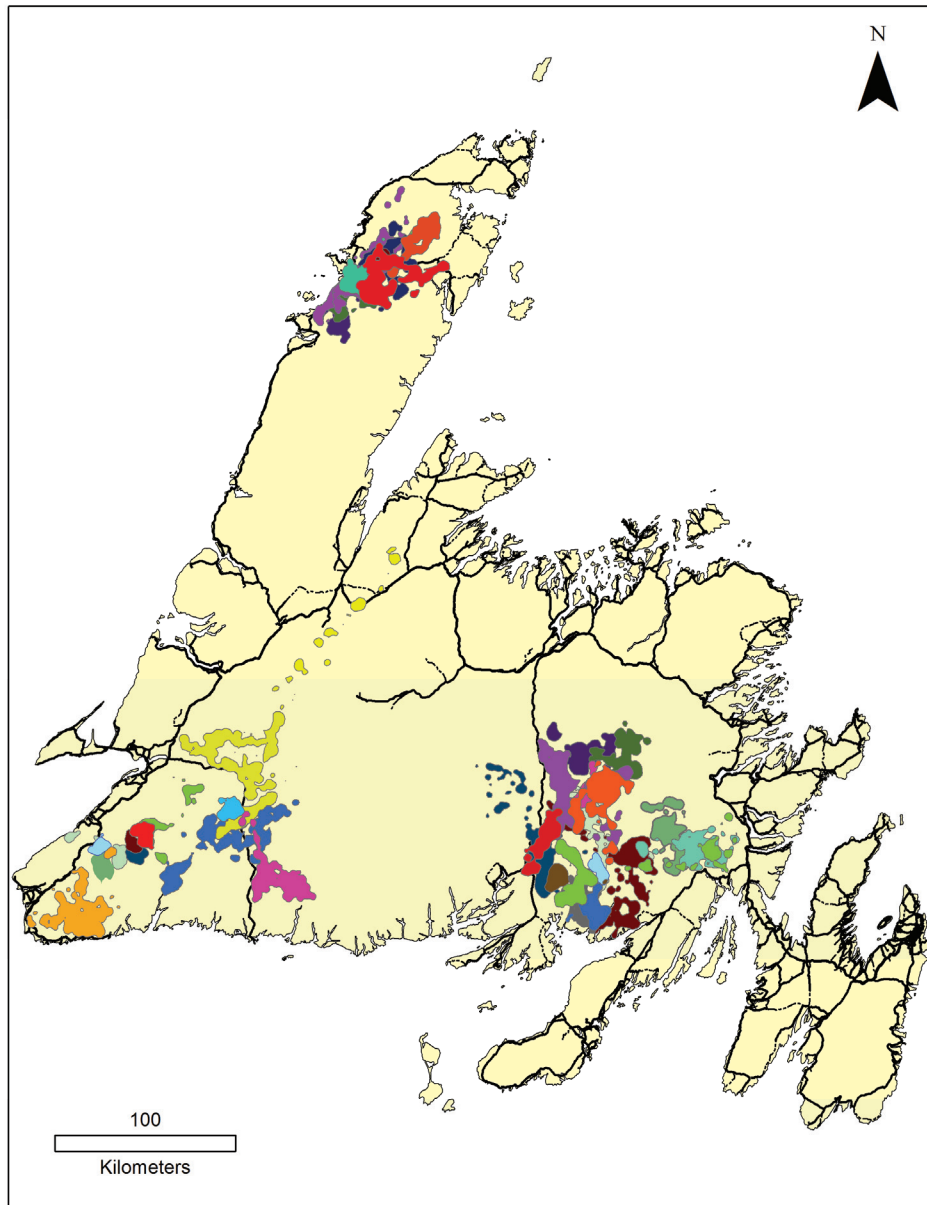
Figure 3. Black bear (*Ursus americanus*) annual home ranges in Newfoundland, 2008–2012. Each coloured outline defines the 95% kernel home range of an individual.

Table 2. Black bear (*Ursus americanus*) annual and seasonal home range sizes, number of samples, and number of animals by study area and sex in Newfoundland, 2008–2012.

Study area	Sex	Area (± SD) (km^2) No. samples (No. animals)				
		Annual	Spring	Summer	Fall	Winter
La Poile	F	145.1 (76.8) 13 (9)	112.7 (73.6) 14 (8)	127.0 (57.4) 15 (10)	55.3 (19.9) 4 (4)	
	M	866.0 (317.0) 5 (4)	651.2 (149.0) 5 (4)	377.4 (177.0) 7 (7)	223.0 (161.2) 2 (2)	
	Total	345.3 (371.8) 18 (13)	254.4 (261.1) 19 (12)	206.7 (159.4) 22 (17)	111.2 (113.8) 6 (6)	
Middle Ridge	F	197.6 (131.0) 10 (5)	169.6 (114.6) 10 (5)	218.7 (102.0) 7 (4)	64.0 (16.0) 5 (4)	40.5 (31.8) 2 (1)
	M	625.1 (162.9) 19 (12)	473.8 (185.1) 21 (14)	389.8 (154.2) 23 (15)	136.0 (79.3) 12 (10)	
	Total	477.7 (251.6) 29 (17)	375.6 (218.3) 31 (19)	349.9 (160.1) 30 (19)	114.8 (74.4) 17 (14)	40.5 (31.8) 2 (1)
Northern Peninsula	F	225.0 (181.6) 7 (4)	149.0 (158.7) 9 (6)	157.2 (97.0) 6 (4)	112.0 (-) 1 (1)	18.0 (-) 1 (1)
	M	44.2 (169.3) 8 (7)	354.6 (111.0) 8 (7)	335.8 (141.7) 5 (4)	250.5 (136.5) 2 (2)	
	Total	363.3 (215.4) 15 (11)	245.8 (170.8) 17 (13)	238.4 (146.4) 11 (8)	204.3 (125.3) 3 (3)	18.0 (-) 1 (1)
Sex totals	F	181.2 (125.4) 30 (18)	139.8 (113.2) 33 (9)	156.4 (85.1) 28 (18)	65.3 (23.1) 10 (9)	33.0 (26.0) 3 (2)
	M	627.5 (217.9) 32 (23)	471.8 (185.1) 34 (25)	379.6 (153.8) 35 (26)	161.2 (98.3) 16 (14)	
Totals		411.6 (286.6) 62 (41)	308.3 (226.5) 67 (34)	280.4 (169.2) 63 (44)	124.3 (90.9) 26 (24)	33.0 (26.0) 3 (2)

Figure 4. Model predicted (± 95% CI) black bears (*Ursus americanus*) annual home range sizes in Newfoundland during 2008–2012 by study area and sex showing the variation between male and female home range sizes by study area.

Seasonal home range

Seasonal home ranges ($n = 159$) were computed for 59 bears (range: 18–1,025 km^2). Few winter home ranges were recorded because of a lack of data points during winter denning. Male home ranges were larger than those of females in spring, summer, and fall (no male data available for winter; $F_{1,53} = 50.22$, $p < 0.0001$; Figure 5A). Home range size differed by season ($F_{1,97} = 23.23$, $p < 0.0001$) with spring and summer being larger than fall and winter (Figure 5B). Seasonal home range size did not differ among study areas ($F_{2,53} = 0.85$, $p = 0.43$).
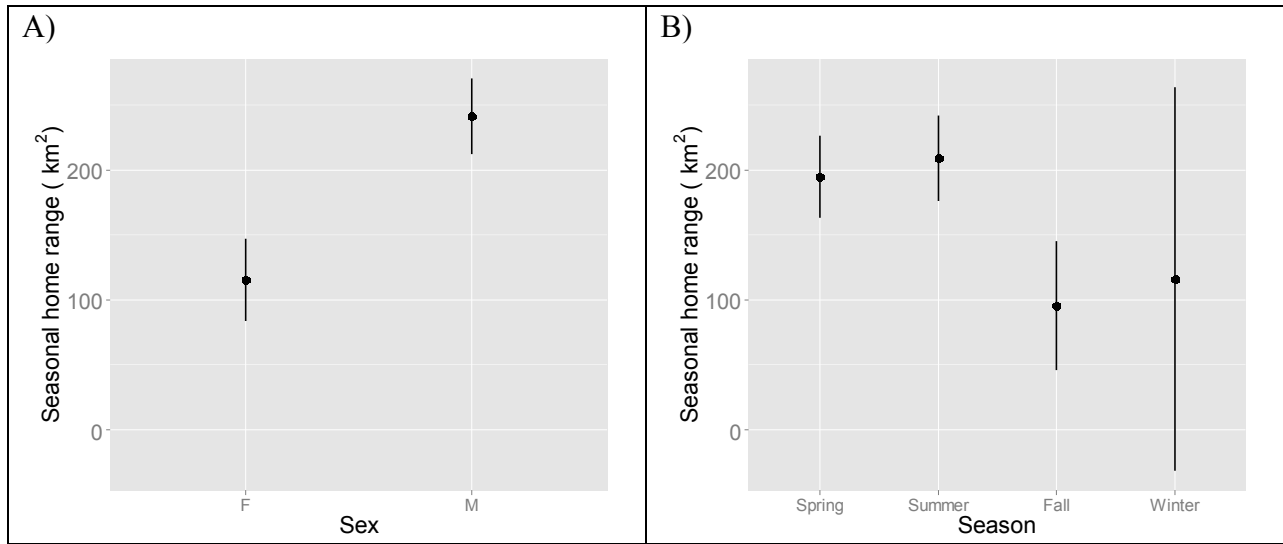
Figure 5. Model predicted (± 95% CI) black bear (*Ursus americanus*) seasonal home range sizes showing differences A) between sexes and B) among seasons in Newfoundland, 2008–2012.

Home range overlap

Individual home ranges were not disjoint; both intra- and inter-sexual overlap was common annually and seasonally (Figure 6).

Site fidelity

A total of 1,356 site fidelity measurements (distances between locations separated by one year, range: 0.01–86.8 km) from 42 bears were analyzed (Table 3). Overall, females displayed greater site fidelity than males ($F_{1,36} = 12.27$, $p = 0.001$; Figure 7A). Seasonal fidelity varied by the interaction of study area and season. In La Poile, fidelity was similar during all seasons. In Middle Ridge, fidelity was generally lower in summer than in fall and winter, whereas in the Northern Peninsula, fidelity was greater in spring and summer than in fall and winter (significant interaction of study area with season: $F_{6,1302} = 4.16$, $p = 0.0004$; Figure 7B).
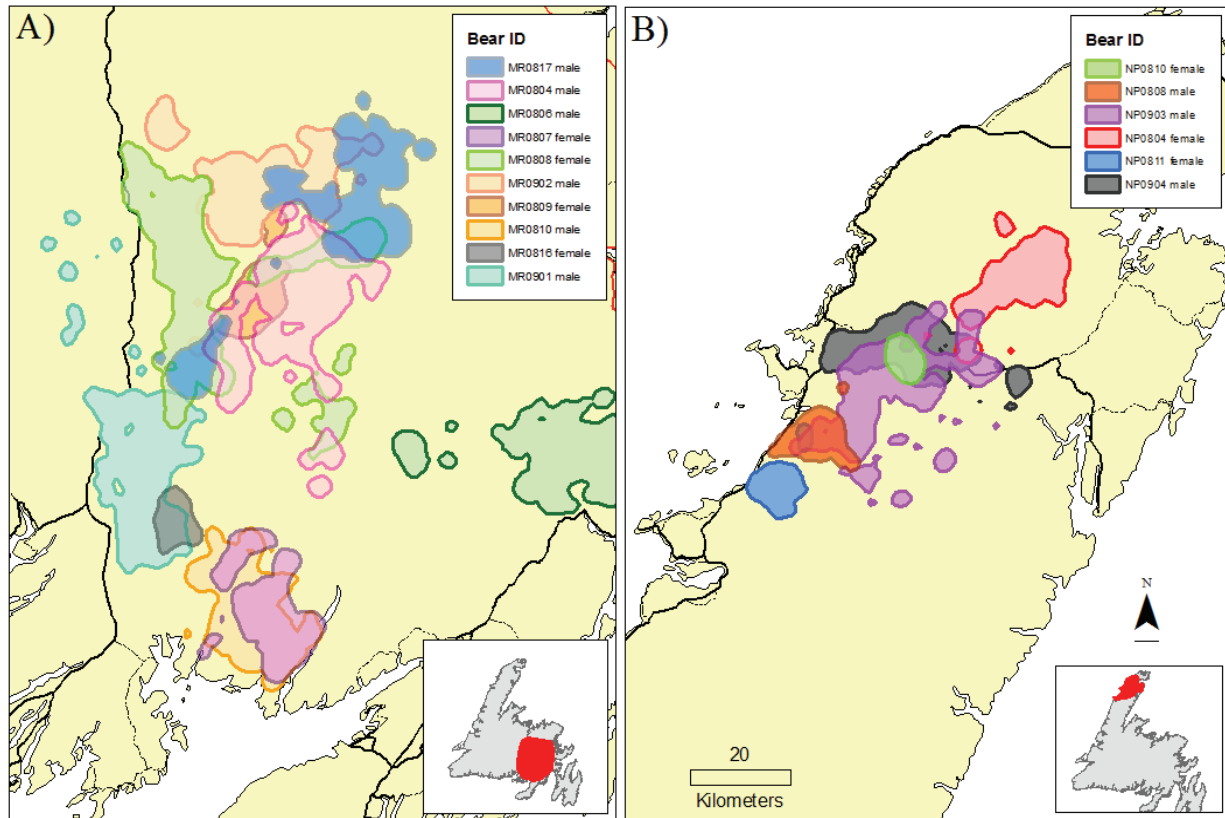
Figure 6. Examples of home range overlap for Newfoundland black bears (*Ursus americanus*) for A) annual home ranges during 2009–2010 in Middle Ridge and B) summer home ranges during 2009 in the Northern Peninsula. Each coloured outline defines the 95% kernel home range of an individual. MR = Middle Ridge and NP = Northern Peninsula.

Table 3. Seasonal site fidelity of black bears (*Ursus americanus*; as measured by distance between locations one year apart), number of samples, and number of animals by study area and sex in Newfoundland, 2008–2013. Smaller distances imply greater site fidelity.

Study area	Sex	Distance (± SD) (km) No. samples (No. animals)				
		Annual	Spring	Summer	Fall	Winter
La Poile	F	5.1 (4.9) 331 (9)	5.5 (4.7) 100 (8)	5.2 (3.8) 151 (6)	4.4 (6.3) 56 (8)	4.7 (8.1) 24 (6)
	M	18.4 (14.9) 72 (4)	21.8 (15.4) 14 (3)	19.0 (15.2) 48 (4)	4.1 (2.0) 6 (2)	20.5 (11.5) 4 (1)
	Total	7.5 (9.2) 403 (13)	7.5 (8.7) 114 (11)	8.5 (10.1) 199 (10)	4.4 (6.0) 62 (10)	7.0 (10.1) 28 (7)
Middle Ridge	F	5.6 (3.9) 255 (6)	6.7 (3.8) 71 (4)	6.8 (3.7) 97 (6)	4.3 (3.4) 49 (5)	1.6 (3.6) 38 (3)
	M	19.4 (20.1) 433 (12)	16.9 (14.7) 113 (8)	20.7 (21.1) 159 (10)	21.7 (23.9) 88 (11)	17.4 (20.0) 73 (10)

Study area	Sex	Distance (± SD) (km) No. samples (No. animals)				
		Annual	Spring	Summer	Fall	Winter
Northern Peninsula	Total	14.2 (17.4) 688 (18)	13.0 (12.7) 184 (12)	15.4 (18.0) 256 (16)	15.5 (21.0) 137 (16)	12.0 (17.9) 111 (13)
	F	7.3 (5.6) 162 (6)	7.4 (5.1) 45 (4)	6.2 (4.9) 69 (4)	9.2 (6.7) 38 (5)	7.0 (7.0) 10 (3)
	M	11.3 (8.4) 103 (5)	10.3 (4.7) 10 (2)	11.2 (8.3) 66 (4)	12.8 (9.7) 25 (3)	2.8 (1.5) 2 (1)
	Total	8.9 (7.1) 265 (11)	7.9 (5.1) 55 (6)	8.7 (52.1) 135 (8)	10.7 (8.1) 63 (8)	6.3 (6.6) 12 (4)
Sex totals	F	5.7 (4.9) 748 (21)	6.3 (4.6) 216 (16)	5.9 (4.1) 317 (16)	5.7 (6.0) 143 (18)	3.4 (5.8) 72 (12)
	M	17.9 (18.3) 608 (21)	16.9 (14.4) 137 (13)	18.1 (18.2) 273 (18)	19.0 (21.6) 119 (16)	17.2 (19.5) 79 (12)
Seasonal totals		11.2 (14.1) 1,356 (42)	10.4 (10.9) 353 (29)	11.6 (14.1) 590 (34)	7.7 (16.5) 262 (34)	10.6 (16.2) 151 (24)
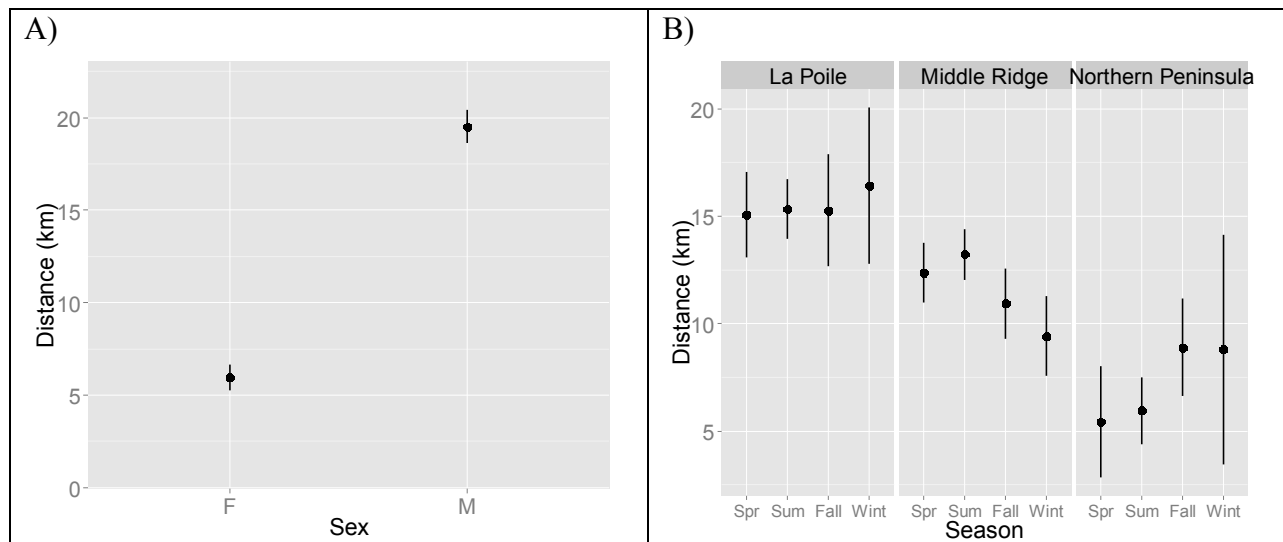
Figure 7. Model predicted (± 95% CI) seasonal black bear (*Ursus americanus*) site fidelity (as indicated by distance between locations one year apart in Newfoundland during 2008–2013, showing A) greater site fidelity of females compared with males and B) different seasonal pattern in each study area. Smaller distances imply greater site fidelity.

Daily movement rate

A total of 3,107 daily movements (range: 0–17.1 km·d^{-1}) were recorded from 87 animals and summarized by season, study area, and sex (Table 4, Figure 8). For both sexes combined, movement rates increased in early spring, plateaued in summer, and then decreased in late fall

with the onset of denning (Figure 8A). Males had greater mean movement rates than females in all seasons, but particularly so in the spring breeding season (significant interaction of sex with season: $F_{3,3008} = 15.92$, $p < 0.0001$; Figure 8A). Seasonal movement rates were generally similar among study areas except that Middle Ridge animals had higher movement rates than either La Poile or the Northern Peninsula during spring (significant interaction of season with study area: $F_{6,3008} = 4.8$, $p = 0.0001$; Figure 8B).

Table 4. Seasonal daily movement rates for black bears (*Ursus americanus*), number of samples, and number of animals by study area and sex in Newfoundland, 2008–2013.

Study area	Sex	Movement rate (± SD) (km·d^{-1}) No. samples (No. animals)				
		Annual	Spring	Summer	Fall	Winter
La Poile	F	2.1 (1.7) 619 (14)	2.3 (1.8) 159 (12)	2.8 (1.4) 293 (14)	1.0 (1.2) 87 (12)	0.2 (0.5) 80 (10)
	M	3.9 (2.9) 250 (9)	6.8 (3.4) 50 (7)	3.8 (2.1) 141 (9)	2.0 (1.7) 31 (6)	1.2 (1.6) 28 (4)
	Total	2.6 (2.3) 869 (23)	3.4 (3.0) 209 (19)	3.1 (1.7) 434 (23)	1.2 (1.4) 118 (18)	0.5 (1.0) 108 (14)
Middle Ridge	F	2.1 (2.1) 570 (19)	3.7 (2.6) 111 (10)	3.0 (1.3) 220 (18)	0.8 (1.7) 114 (15)	0.2 (0.5) 125 (12)
	M	3.4 (2.7) 1,013 (25)	6.0 (2.7) 229 (19)	3.7 (2.0) 405 (24)	1.9 (1.8) 178 (21)	1.1 (1.8) 201 (18)
	Total	2.9 (2.6) 1,583 (44)	5.2 (2.9) 340 (29)	3.4 (1.8) 625 (42)	1.5 (1.8) 292 (36)	0.8 (1.5) 326 (30)
Northern Peninsula	F	1.8 (1.8) 332 (8)	2.0 (2.1) 83 (6)	2.8 (1.6) 127 (8)	1.1 (1.1) 69 (8)	0.2 (0.5) 53 (6)
	M	3.4 (2.5) 323 (12)	5.0 (2.9) 75 (8)	3.5 (1.9) 159 (12)	2.4 (2.4) 61 (9)	1.1 (1.4) 28 (7)
	Total	2.6 (2.3) 655 (20)	3.4 (2.9) 158 (14)	3.2 (1.8) 286 (20)	1.7 (1.9) 130 (17)	0.5 (1.0) 81 (13)
Sex totals	F	2.0 (1.9) 1,521 (41)	2.6 (2.3) 353 (28)	2.9 (2.7) 640 (40)	0.9 (1.4) 270 (35)	0.2 (0.5) 258 (28)
	M	3.5 (2.7) 1,586 (46)	5.9 (2.9) 354 (34)	3.6 (2.0) 705 (45)	2.0 (1.9) 270 (36)	1.1 (1.7) 257 (29)
Seasonal totals		2.8 (2.4) 3,107 (87)	4.3 (3.1) 707 (62)	3.3 (1.8) 1,345 (85)	1.5 (3.2) 540 (71)	0.7 (1.8) 515 (57)
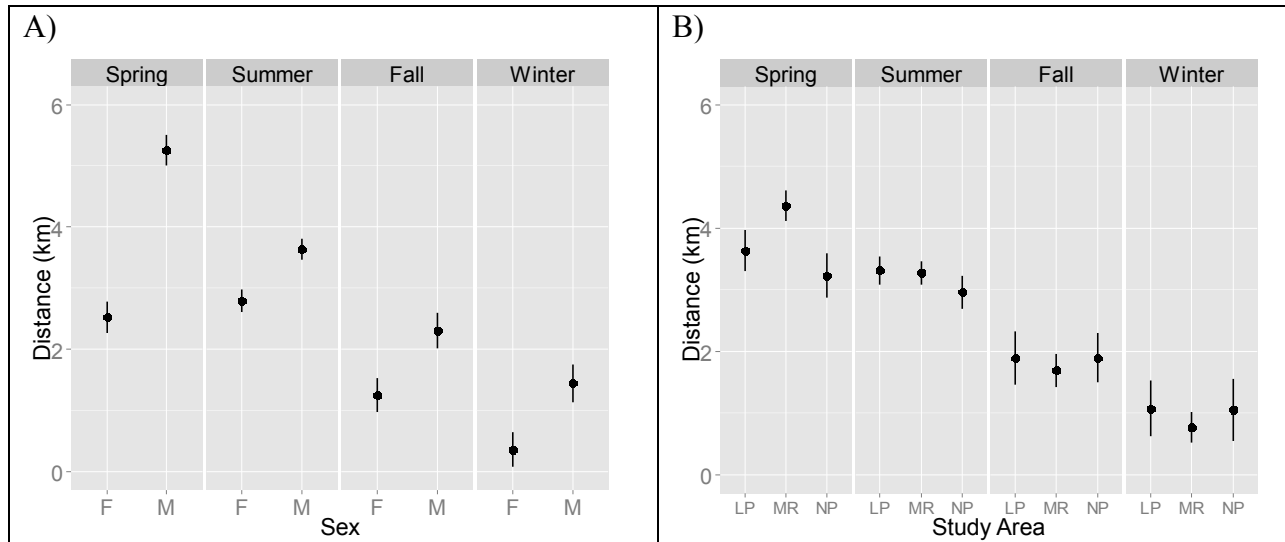
Figure 8. Model predicted (± 95% CI) seasonal black bear (*Ursus americanus*) daily movement rates in Newfoundland, 2008–2013, by A) sex and season showing the greatest difference between males and females in spring compared with other seasons and by B) study area and season showing greater differences among study areas in spring. LP = La Poile, MR = Middle Ridge, and NP = Northern Peninsula.

Coyote

Individual coyotes (*n* = 79; 45 males, 34 females) were tracked during 2008–2012 for an average of 245 ± 198 (range: 7–890) days producing 68,286 positions (Figure 9, Table 5). Of the 61 animals that were tracked long enough to assess behaviour mode, 15 (24.6%) were transients and the remainder residents. Transient coyotes (*n* = 15; 13 males, 2 females) were found in all study areas and often made direct, long-distance movements covering the breadth of the island, interspersed with periods of localized residency lasting 1–12 months (Figure 10). Several transient coyotes in the Northern Peninsula made short excursions over sea ice in winter; however, one individual spent almost 3 weeks on the ice while traversing 180 km (straight line distance) from the tip of the Northern Peninsula to the Baie Verte Peninsula via the Grey Islands (Figure 11).
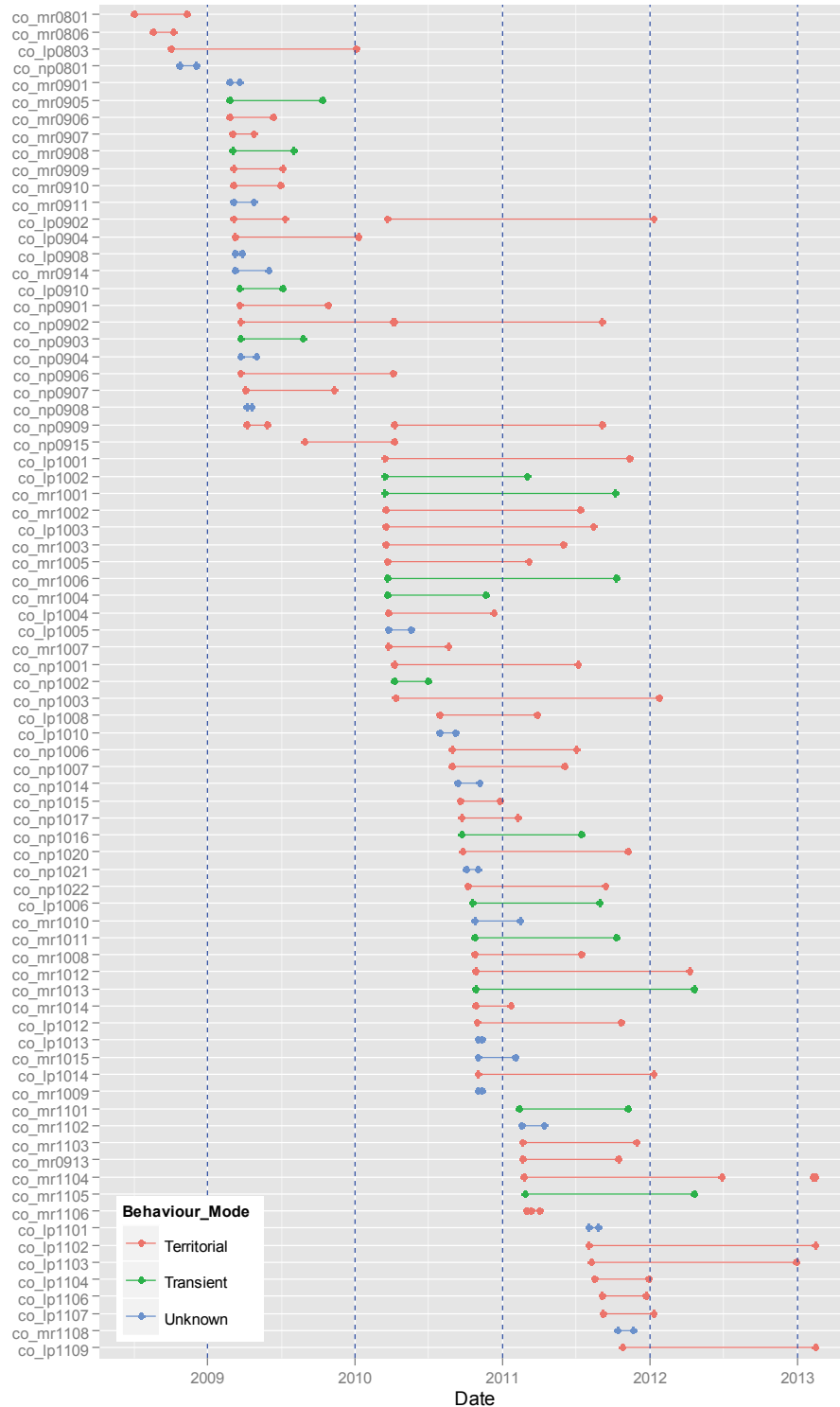
Figure 9. Duration of collaring and behavioural mode for 79 coyotes (*Canis latrans*) in Newfoundland, 2008–2013. Note continuous data were not always available between collar deployment and removal because of battery depletion or collar failure. LP = La Poile, MR = Middle Ridge, and NP = Northern Peninsula.
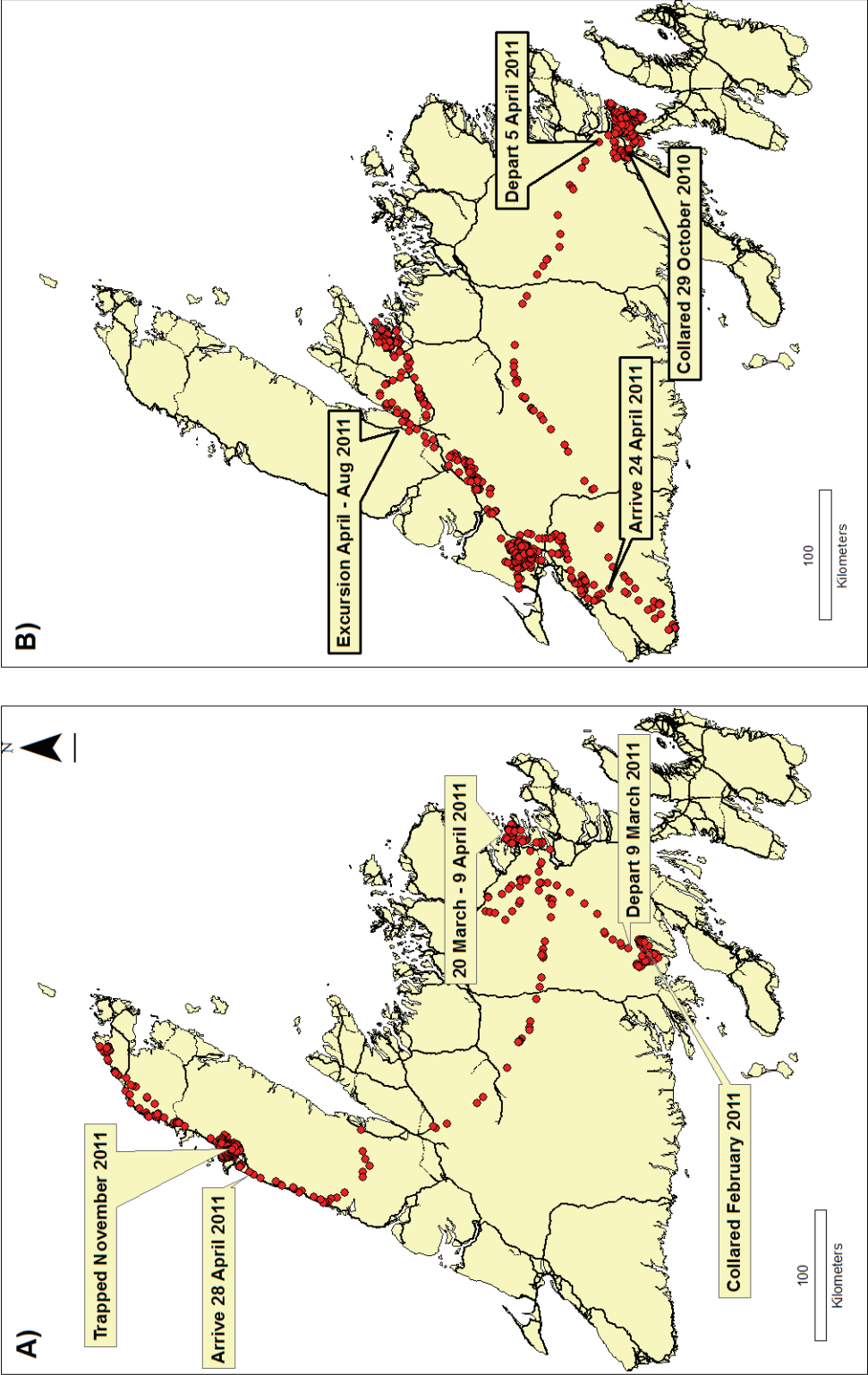
Figure 10. Long-distance movements interspersed with periods of local residency for transient coyotes (*Canis latrans*) A) MR1101 and B) MR1013 in Newfoundland during 2010–2011.
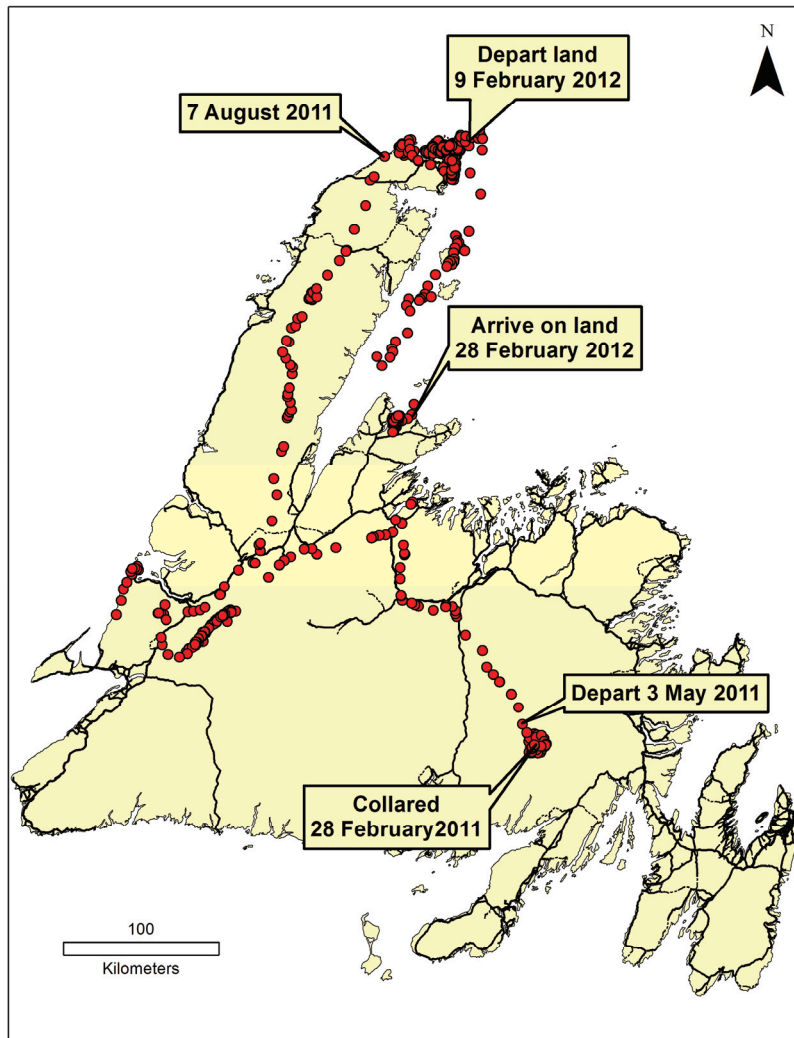
Figure 11. Use of ice during almost 3 weeks at sea during February 2012 by transient coyote (*Canis latrans*) MR1105 originally collared in Middle Ridge in 2011.

Table 5. Summary of coyote (*Canis latrans*) telemetry data in Newfoundland during 2008–2013 showing number of animals collared, number of positional fixes obtained, and mean number of days monitored by study area and sex.

Study area	Sex	Number of animals	Number of fixes	Mean (± SD) monitoring days
La Poile	F	6	6,193	243 (140)
	M	17	16,445	265 (224)
	Total	23	22,638	259 (203)
Middle Ridge	F	19	11,795	172 (145)
	M	15	15,174	291 (200)
	Total	34	26,969	224 (179)
Northern Peninsula	F	9	10,060	384 (283)
	M	13	8,619	180 (127)
	Total	22	18,679	264 (224)
Sex totals	F	34	28,048	240 (203)
	M	45	40,238	249 (194)
Overall total		79	68,286	245 (198)

Home range size

Annual home range

Annual home range size ($n = 27$ from 25 animals) varied greatly between resident (range: 53–558 km^2; Figure 12A) and transient (range: 198–2,358 km^2; Figure 12B) coyotes and, to a lesser extent, between sexes and among study areas (Table 6). Transient coyotes ($n = 7$ or 25.9% of individuals for which annual home range was calculated) had larger mean annual home ranges than resident coyotes by a factor of almost five ($F_{1,14} = 84.22, p < 0.0001$). Although many resident males had larger home ranges than resident females, there was also great variation and thus no statistically significant difference between the sexes ($F_{1,14} = 1.71, p = 0.21$). Likewise, there were no significant differences among residents by study area ($F_{1,2} = 0.24, p = 0.79$).
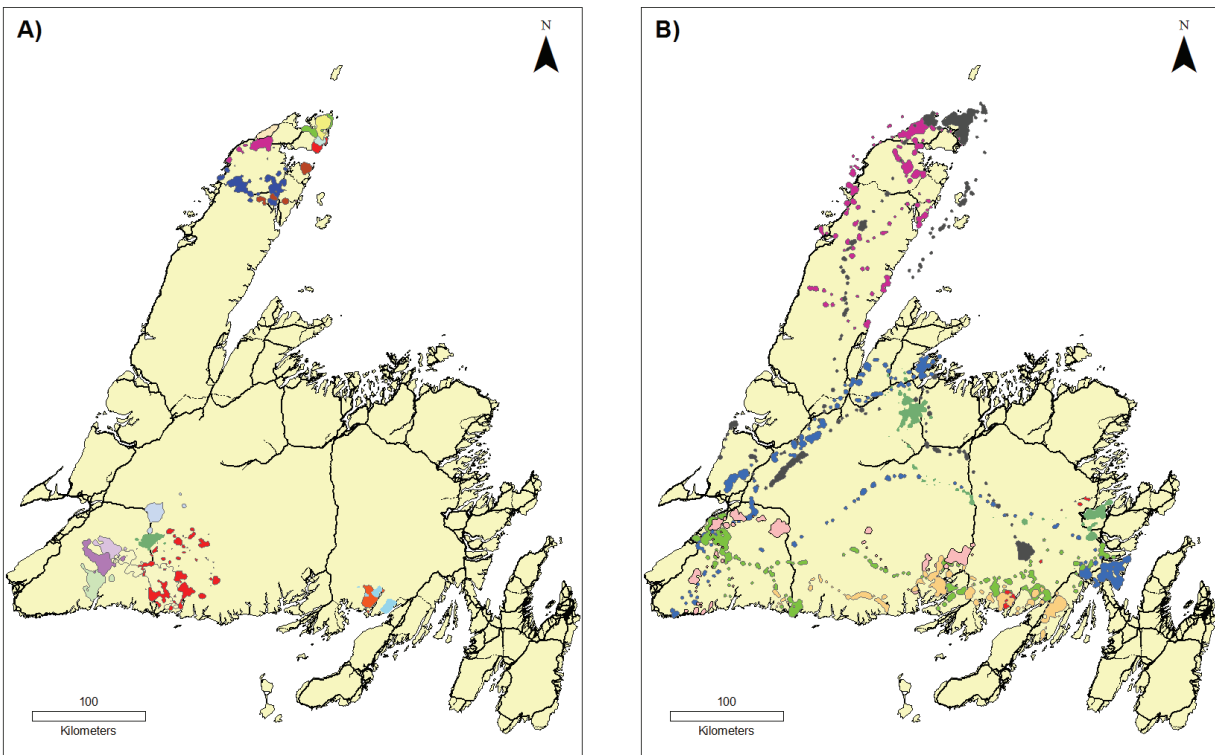
Figure 12. Annual home ranges for A) resident, and B) transient coyotes (*Canis latrans*) in Newfoundland, 2008–2011. Each coloured outline defines the 95% kernel home range of an individual.

Table 6. Coyote (*Canis latrans*) annual home range sizes, number of home ranges, and number of animals summarized by study area, behaviour mode, and sex in Newfoundland during 2008–2011.

Study area	Sex	Area (± SD) (km^2) No. samples (No. animals)	
		Residents	Transients (males only)
La Poile	F	204.0 (-) 1 (1)	
	M	328.8 (50.1) 5 (4)	1,263.0 (175.4) 2 (2)
	Total	308.0 (67.8) 6 (5)	
Middle Ridge	F	207.3 (168.4) 3 (3)	

| Study area | Sex | Area (± SD) (km²) No. samples (No. animals) | |
		Residents	Transients (males only)
	M	235.5 (17.7) 2 (2)	1,633.0 (972.5) 4 (4)
	Total	218.6 (120.4) 5 (5)	
Northern Peninsula	F	157.3 (77.6) 7 (6)	
	M	339.0 (309.7) 2 (2)	1,460.0 (-)
	Total	197.7 (151.4) 9 (8)	1 (1)
Sex totals	F	175.2 (99.5) 11 (10)	
	M	310.0 (122.9) 9 (8)	
Overall total		316.7 (292.0) 20 (18)	1,502.6 (713.3) 7 (7)

Seasonal home range

Seasonal home ranges for resident ($n = 102$ for 40 animals, range: 33–601.0 km²) and transient ($n = 33$ for 13 animals, range: 78–1,099 km²) coyotes are presented in Table 7.

Residents. Home range size varied seasonally ($F_{3,50} = 9.77$, $p < 0.0001$), with spring ranges being the smallest, summer and fall intermediate, and winter the largest (Table 7, Figure 13A). Males had larger home ranges than females in all seasons ($F_{1,34} = 10.23$, $p = 0.003$; Figure 13B). Seasonal home range also varied by study area ($F_{2,34} = 12.93$, $p = 0.0001$), with La Poile home ranges being larger than those in Middle Ridge, which were larger than those in the Northern Peninsula (Figure 13C). However, the ratio of males to females in each study area was not consistent, which may account for the observed differences in average home range size in each area, since males have larger home ranges than females.

Residents vs. transients. As expected, transient coyotes had much larger home ranges than resident coyotes in all seasons although this was not the case in fall (significant interaction of season with behaviour mode: $F_{3,79} = 4.83$, $p = 0.0039$; Figure 13D).

Table 7. Coyote (*Canis latrans*) seasonal home range sizes, number of samples, and number of animals by behaviour mode, study area, and sex in Newfoundland, 2008–2012.

		Residents				Transients (males only)			
		Area (± SD) (km^2) No. samples (No. animals)				Area (± SD) (km^2) No. samples (No. animals)			
Study area	Sex	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
La Poile	F	214.0 (159.1) 3 (3)	310.3 (251.8) (3) 3	150.0 (61.2) 4 (3)	214.0 (8.5) 2 (2)				
	M	148.3 (44.5) 6 (3)	215.6 (50.8) 5 (4)	236.9 (78.4) 9 (8)	252.8 (94.1) 5 (5)	629.7 (196.0) 3 (3)	593.0 (-) 1 (1)	308.0 (-) 1 (1)	637.0 (-) 1 (1)
	Total	170.6 (92.9) 9 (6)	251.1 (148.3) 9 (8)	210.2 (82.3) 13 (11)	241.7 (79.2) 7 (7)				
Middle Ridge	F	124.8 (135.1) 4 (4)	109.6 (49.4) 5 (5)	103.5 (94.0) 2 (2)	129.0 (124.5) 2 (2)				
	M	170.6 (31.9) 5 (4)	159.0 (19.0) 3 (3)	160.7 (46.5) 3 (3)	196.5 (34.6) 2 (2)	538.2 (290.7) 8 (7)	804.8 (368.8) 6 (5)	180.8 (62.9) 4 (4)	734.2 (416.7) 4 (3)
	Total	150.2 (99.1) 9 (8)	128.1 (46.4) 8 (8)	137.8 (65.4) 5 (5)	162.8 (84.2) 4 (4)				
Northern Peninsula	F	97.6 (45.0) 7 (6)	80.1 (35.4) 8 (6)	56.4 (21.5) 5 (4)	115.0 (86.0) 3 (3)				
	M	102.2 (39.3) 4 (3)	125.5 (30.4) 2 (2)	124.5 (74.5) 6 (6)	319.2 (196.7) 4 (4)	766.0 (326.6) 3 (3)		90.0 (-) 1 (1)	411.0 (-) 1 (1)
	Total	99.3 (41.0) 11 (9)	89.2 (38.0) 10 (8)	93.5 (65.0) 11 (10)	231.7 (183.6) 7 (7)				
Sex totals	F	130.3 (106.0) 14 (13)	132.5 (132.8) 16 (14)	99.0 (64.4) 11 (9)	147.3 (84.7) 7 (7)				
	M	143.6 (87.2) 15 (10)	180.6 (53.3) 10 (9)	186.7 (87.2) 18 (17)	266.7 (132.1) 11 (11)	606.6 (276.9) 14 (13)	774.6 (346.0) 7 (6)	186.8 (84.9) 6 (6)	664.2 (348.0) 6 (5)
Seasonal totals		137.2 (79.4) 29 (23)	151.0 (11.4) 26 (23)	153.4 (89.3) 29 (26)	220.3 (128.0) 18 (18)	606.6 (276.9) 14 (13)	774.6 (346.0) 7 (6)	186.8 (84.9) 6 (6)	664.2 (348.0) 6 (5)
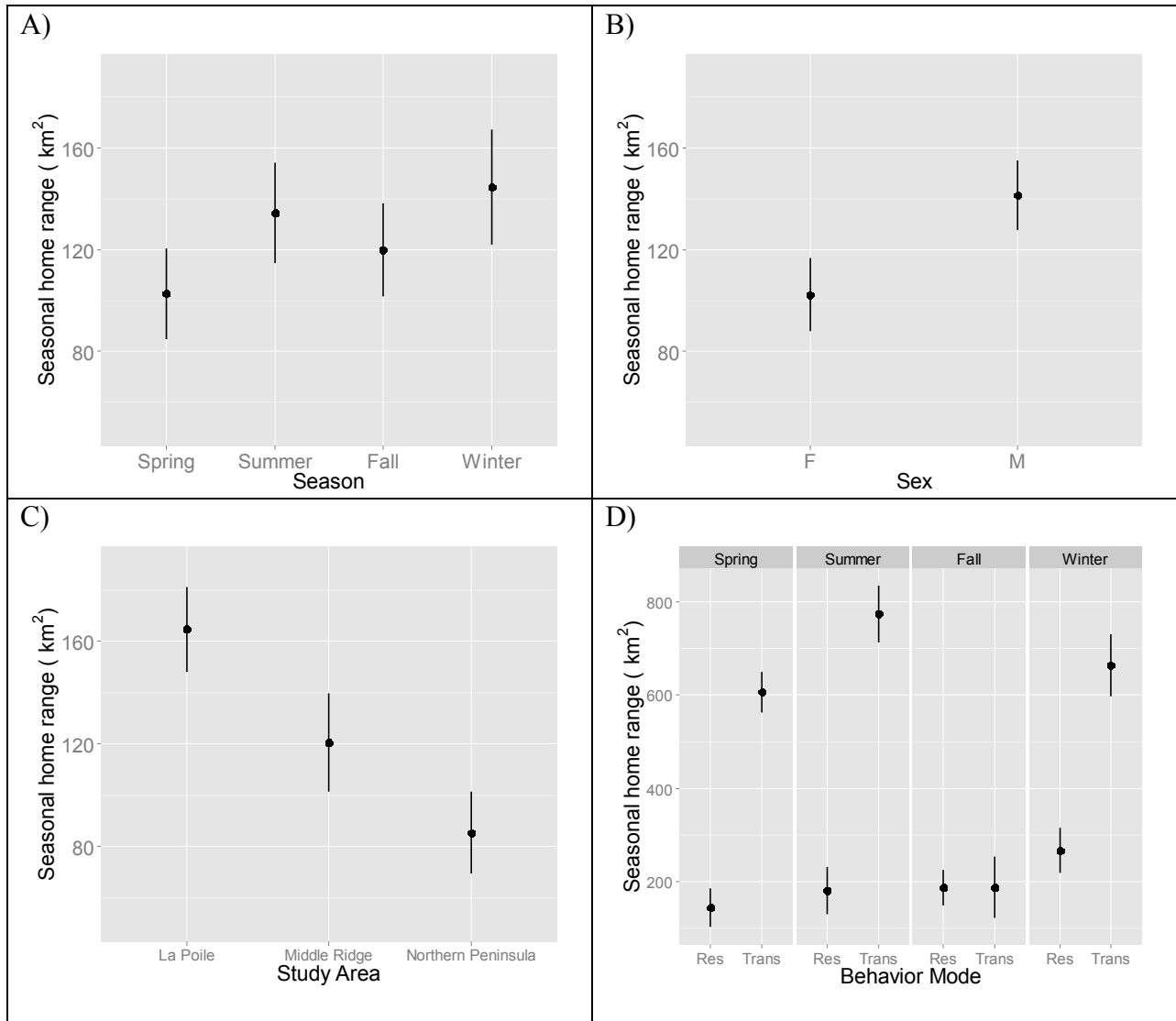
Figure 13. Model predicted (± 95% CI) seasonal home range sizes for coyotes (*Canis latrans*) in Newfoundland by A) season, B) sex, and C) study area for resident coyotes and D) behaviour mode and season for transient coyotes during 2008–2012. Note the different *y*-axis scale for panel D. Res = resident and Trans = transient.

Home range overlap

Resident coyote annual (Figure 12) and seasonal home ranges showed little overlap among individuals, but did overlap with transient coyote ranges (Figures 12 & 14). However, we observed four cases (2 in Middle Ridge, 1 each in La Poile and the Northern Peninsula) of a collared male and female traveling together (Figure 15), which we interpret as mated pairs (Atwood and Weeks 2003), although we cannot rule out the possibility that these pairs were part of larger groups that also contained uncollared individuals (Patterson and Messier 2001).
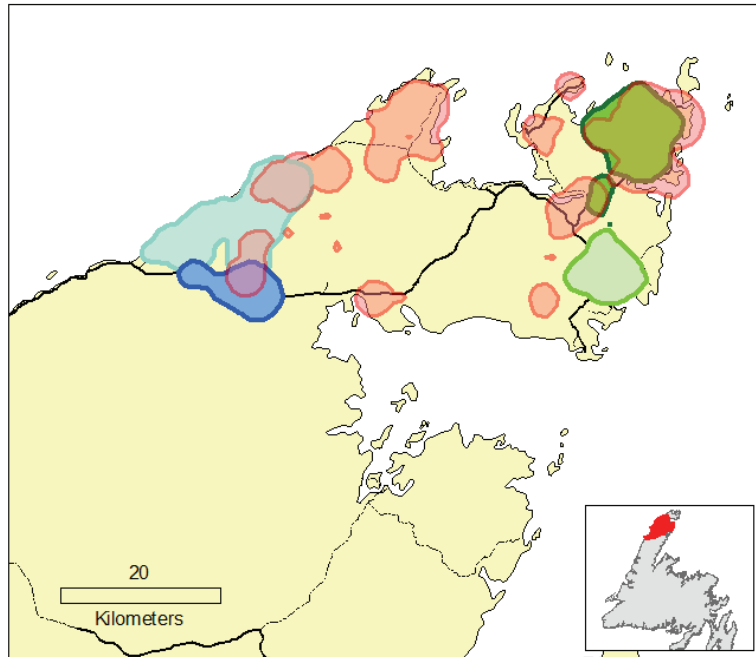
Figure 14. Example of non-overlapping home ranges of four resident coyotes (*Canis latrans*; blues and greens) and overlap with the home range of one transient coyote (red) on the Northern Peninsula in spring 2009.
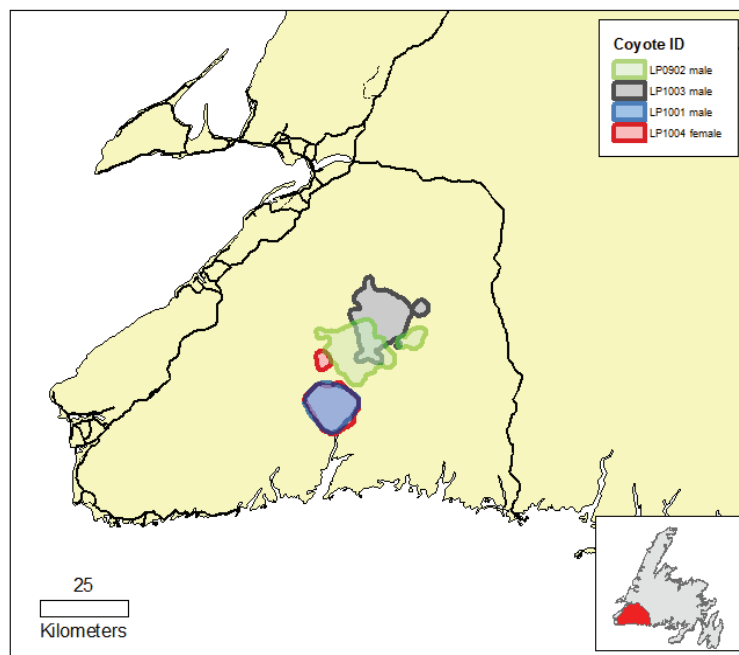
Figure 15. Summer 2010 home ranges of four coyotes (*Canis latrans*) in La Poile illustrating coincident space use by a mated pair (LP1001 and LP1004) and less overlapping home ranges of other individuals. LP = La Poile.

Site fidelity

A total of 589 (resident = 473, transient = 116) site fidelity measurements (distances between locations separated by one year) were analyzed for 16 coyotes (resident: $n = 12$, range: 1.0–25.1 km; transient: $n = 4$, range: 17.8–350.4 km; Tables 8 & 9). Resident females displayed greater site fidelity than males ($F_{1,6} = 8.06$, $p = 0.03$; Figure 16A). Neither season ($F_{3,455} = 1.50$, $p = 0.21$) nor study area ($F_{2,6} = 1.00$, $p = 0.41$) had a significant effect on resident coyote site fidelity (not shown). Resident coyotes displayed far greater site fidelity than transient coyotes ($F_{1,9} = 88.9$, $p < 0.0001$; Table 8, Figure 16B).

Table 8. Overall site fidelity of coyote (*Canis latrans*; as measured by distance between locations one year apart), number of samples, and number of animals by behaviour mode, study area, and sex in Newfoundland during 2008–2012. Smaller distances imply greater site fidelity.

		Distance (± SD) (km) No. samples (No. animals)	
Study area	Sex	Residents	Transients (males only)
La Poile	F	5.2 (1.4) 19 (1)	
	M	7.7 (3.3) 152 (3)	
	Total	7.4 (3.2) 171 (4)	
Middle Ridge	F	3.4 (0.8) 34 (1)	
	M	7.1 (2.6) 47 (2)	199.1 (83.2) 116 (4)
	Total	5.6 (2.7) 81 (3)	199.1 (83.2) 116 (4)
Northern Peninsula	F	5.2 (3.4) 206 (4)	
	M	7.3 (1.3) 15 (1)	
	Total	5.3 (3.4) 221 (5)	
Sex totals	F	4.9 (3.1) 259 (6)	
	M	7.5 (3.1) 214 (6)	199.1 (83.2) 116 (4)
Overall total		6.1 (3.4) 473 (12)	199.1 (83.2) 116 (4)

Table 9. Seasonal site fidelity of coyote (*Canis latrans*; as measured by distance between locations one year apart), number of samples, and number of animals by behaviour mode, study area, and sex in Newfoundland during 2008–2012. Smaller distances imply greater site fidelity.

		Residents — Distance (± SD) (km), No. samples (No. animals)				Transients (males only) — Distance (± SD) (km), No. samples (No. animals)			
Study area	Sex	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
La Poile	F			4.9 (1.5) 12 (1)	5.8 (1.2) 7 (1)				
	M	6.0 (1.7) 46 (3)	7.3 2.4 40 (3)	11.1 (3.7) 20 (2)	8.3 (3.8) 46 (3)				
	Total	6.0 (1.7) 46 (3)	7.3 2.4 40 (3)	8.8 (4.3) 32 (3)	8.0 (3.6) 53 (4)				
Middle Ridge	F			3.3 (0.8) 7 (1)	3.5 (0.8) 27 (1)				
	M	5.9 (1.6) 22 (2)	4.6 (1.1) 2 (1)		8.5 (2.8) 23 (2)	152.8 (47.8) 19 (2)	138.4 (34.8) 32 (2)	268.4 (90.0) 10 (3)	237.9 (101.6) 55 (4)
	Total	5.9 (1.6) 22 (2)	4.6 (1.1) 2 (1)	3.3 (0.8) 7 (1)	5.8 (3.2) 50 (3)	152.8 (47.8) 19 (2)	138.4 (34.8) 32 (2)	268.4 (90.0) 10 (3)	237.9 (101.6) 55 (4)
Northern Peninsula	F	4.9 (2.6) 52 (3)	4.6 (2.5) 61 (4)	5.0 (3.0) 28 (3)	6.0 (4.6) 65 (3)				
	M	7.5 (1.0) 10 (1)			6.9 (2.0) 5 (1)				
	Total	5.3 (2.6) 62 (4)	4.6 (2.5) 61 (4)	5.0 (3.0) 28 (3)	6.0 (4.5) 70 (4)				
Sex totals	F	4.9 (2.6) 52 (3)	4.6 (2.5) 61 (4)	4.7 (2.5) 47 (5)	5.3 (3.9) 99 (5)				
	M	6.1 (1.7) 78 (6)	7.1 (2.4) 42 (4)	11.1 (3.7) 20 (2)	8.3 (3.4) 74 (6)	152.8 (47.8) 19 (2)	138.4 (34.8) 32 (2)	268.4 (90.0) 10 (3)	237.9 (101.6) 55 (4)
Seasonal totals		5.7 (2.2) 130 (9)	5.6 (2.7) 103 (8)	6.6 (4.1) 67 (7)	6.6 (4.0) 173 (11)	152.8 (47.8) 19 (2)	138.4 (34.8) 32 (2)	268.4 (90.0) 10 (3)	237.9 (101.6) 55 (4)
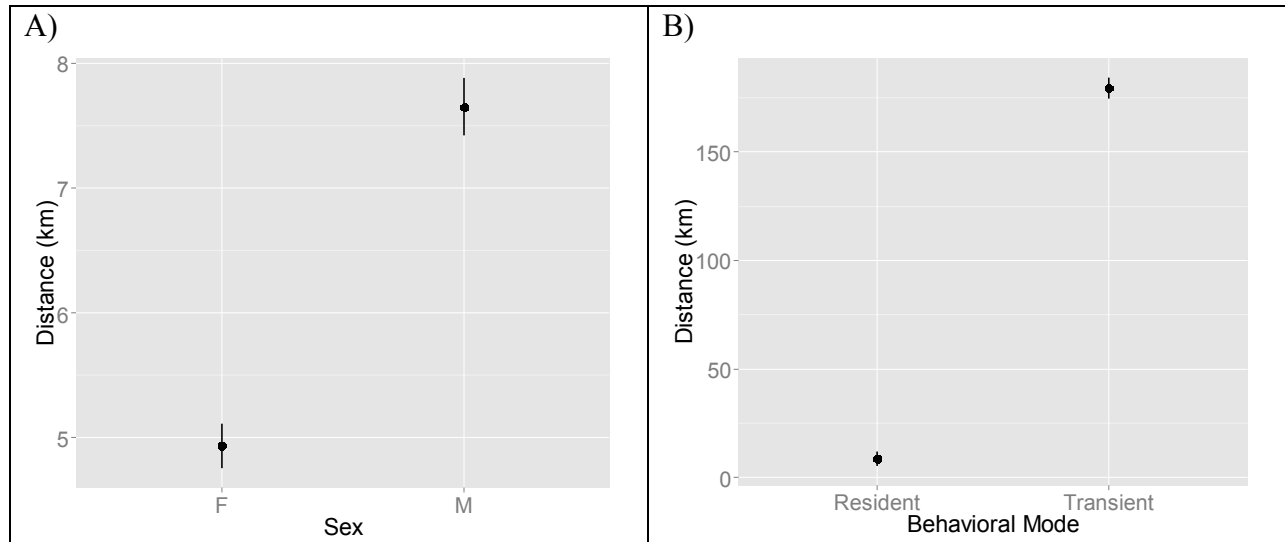
Figure 16. Model predicted (± 95% CI) coyote (*Canis latrans*) site fidelity (as indicated by distance between locations one year apart) in Newfoundland during 2008–2012 by A) sex showing greater site fidelity for females compared with males (residents only) and B) behavioural mode showing greater site fidelity for resident coyotes. Note the different *y*-axis scales for each panel. Smaller distance implies greater site fidelity.

Daily movement rate

A total of 2,192 (resident: $n = 1,637$, transient: $n = 555$) daily movements were recorded from 59 (resident: $n = 46$, transient: $n = 13$) coyotes and were summarized by season, study area, behaviour mode, and sex (Tables 10 & 11). Overall, movement rates for resident coyotes (mean: 4.1 ± 4.0 km·d^{-1}, range: 0.1–37.1 km·d^{-1}) were broadly similar to those for transient coyotes (mean: 4.9 ± 4.3 km·d^{-1}, range: 0.1–29.4 km·d^{-1}). Resident males had greater movement rates than females ($F_{1,40} = 4.33$, $p = 0.044$; Figure 17A). The seasonal pattern of movement rate for resident coyotes differed by study area (significant interaction of season with study area: $F_{6, 1579} = 3.23$, $p = 0.0037$; Figure 17B). The difference between daily movement rate for transient versus resident coyotes varied by season (significant interaction of behaviour mode with season: $F_{3,1499} = 19.53$, $p < 0.0001$). On a seasonal basis, movement rates for transient coyotes were larger than those for resident coyotes during spring, summer, and winter, but similar during fall (Figure 17C).

Table 10. Overall daily movement rates for coyotes (*Canis latrans*), number of samples, and number of animals by behaviour mode, study area, and sex in Newfoundland during 2008–2012.

Study area	Sex	Movement rate (± SD) (km·d⁻¹) No. samples (No. animals)	
		Residents	Transients (males only)
La Poile	F	4.3 (3.6) 178 (5)	
	M	5.0 (4.8) 434 (10)	5.1 (3.4) 114 (3)
	Total	4.8 (4.5) 612 (15)	5.1 (3.4) 114 (3)
Middle Ridge	F	3.9 (3.9) 274 (12)	
	M	4.9 (4.2) 178 (5)	5.3 (4.3) 364 (7)
	Total	4.3 (4.0) 452 (17)	5.3 (4.3) 364 (7)
Northern Peninsula	F	2.9 (2.7) 360 (7)	
	M	4.0 (3.8) 213 (7)	5.4 (4.5) 77 (3)
	Total	3.3 (3.2) 573 (14)	5.4 (4.5) 77 (3)
Sex totals	F	3.6 (3.4) 812 (24)	
	M	4.7 (4.5) 825 (22)	5.3 (4.1) 555 (13)
Overall total		4.1 (4.0) 1637 (46)	5.3 (4.1) 555 (13)

Table 11. Seasonal daily movement rates for coyotes (*Canis latrans*), number of samples, and number of animals by behaviour mode, study area, and sex in Newfoundland during 2008–2012.

		Residents				Transients (males only)			
		Movement rate (± SD) (km·d⁻¹) No. samples (No. animals)				Movement rate (± SD) (km·d⁻¹) No. samples (No. animals)			
Study area	Sex	Spring	Summer	Fall	Winter	Spring	Summer	Fall	Winter
La Poile	F	4.5 (3.9) 27 (4)	5.0 (4.3) 41 (4)	3.3 (2.8) 42 (5)	4.4 (3.5) 68 (5)				
	M	5.0 (3.3) 66 (6)	5.0 (4.5) 111 (10)	3.9 (4.4) 89 (10)	5.5 (5.7) 168 (10)	5.8 (3.0) 24 (3)	4.9 (2.7) 24 (3)	2.7 (1.4) 15 (2)	5.5 (3.9) 51 (3)
	Total	4.9 (3.5) 93 (10)	5.0 (4.4) 152 (14)	3.7 (3.9) 131 (15)	5.2 (5.2) 236 (15)	5.8 (3.0) 24 (3)	4.9 (2.7) 24 (3)	2.7 (1.4) 15 (2)	5.5 (3.9) 51 (3)
Middle Ridge	F	2.3 (2.4) 51 (8)	2.9 (2.4) 68 (8)	3.2 (2.3) 31 (7)	5.3 (4.8) 124 (10)				
	M	4.0 (4.1) 42 (4)	5.6 (4.0) 36 (3)	5.2 (3.8) 26 (4)	4.9 (4.5) 74 (5)	6.4 (3.9) 67 (7)	5.4 (3.8) 99 (7)	3.1 (2.3) 45 (6)	5.5 (5.0) 153 (7)
	Total	3.1 (3.3) 93 (12)	3.9 (3.3) 104 (11)	4.2 (3.2) 57 (11)	5.2 (4.7) 198 (15)	6.4 (3.9) 67 (7)	5.4 (3.8) 99 (7)	3.1 (2.3) 45 (6)	5.5 (5.0) 153 (7)
Northern Peninsula	F	2.4 (2.5) 69 (7)	3.3 (3.2) 112 (7)	2.2 (2.5) 53 (7)	3.2 (2.4) 126 (7)				
	M	2.9 (2.6) 35 (4)	3.8 (3.0) 40 (7)	3.1 (2.6) 45 (7)	4.9 (4.7) 93 (7)	6.8 (3.6) 24 (3)	6.1 (4.4) 13 (2)	1.6 (1.0) 8 (1)	5.0 (5.1) 32 (3)
	Total	2.6 (2.5) 104 (11)	3.4 (3.2) 152 (14)	2.6 (2.5) 98 (14)	3.9 (3.7) 219 (14)	6.8 (3.6) 24 (3)	6.1 (4.4) 13 (2)	1.6 (1.0) 8 (1)	5.0 (5.1) 32 (3)
Sex totals	F	2.8 (2.9) 147 (19)	3.5 (3.3) 221 (19)	2.8 (2.6) 126 (19)	4.3 (3.8) 318 (22)				
	M	4.2 (3.5) 143 (14)	4.8 (4.1) 187 (20)	3.9 (3.9) 160 (21)	5.2 (5.2) 335 (22)	6.0 (3.6) 115 (13)	5.3 (3.7) 136 (12)	2.9 (2.1) 68 (9)	5.5 (4.8) 236 (13)
Seasonal totals		3.5 (3.3) 290 (33)	4.1 (3.8) 408 (39)	3.4 (3.4) 286 (40)	4.8 (4.6) 653 (44)	6.0 (3.6) 115 (13)	5.3 (3.7) 136 (12)	2.9 (2.1) 68 (9)	5.5 (4.8) 236 (13)
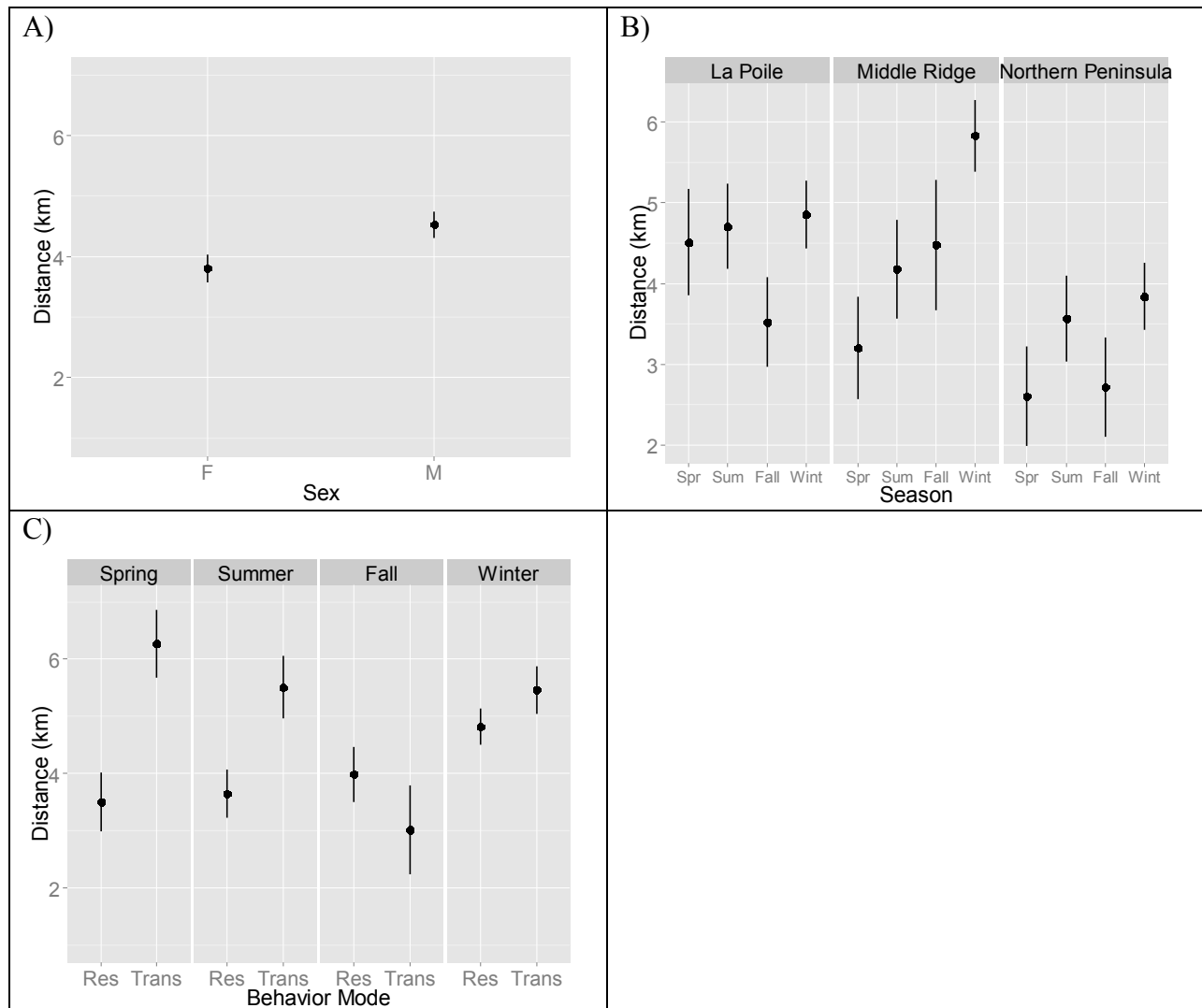
Figure 17. Model predicted (± 95% CI) coyote (*Canis latrans*) daily movement rates in Newfoundland during 2008–2012 by A) sex, showing larger movement rates for resident males, B) differing seasonal patterns for each study area, and C) variable seasonal patterns for resident versus transient coyotes. Panels A and B show residents only while panel C compares residents with transients. Res = resident and Trans = transient.

Lynx

Fewer lynx data were available in comparison with coyotes and bears; a total of 13 lynx provided 3,922 telemetry data points (Figure 18, Table 12). Most animals were tracked for relatively short periods, with an average of 112 ± 124 (range: 61–214) days, because of the inability to relocate animals for remote collar download.
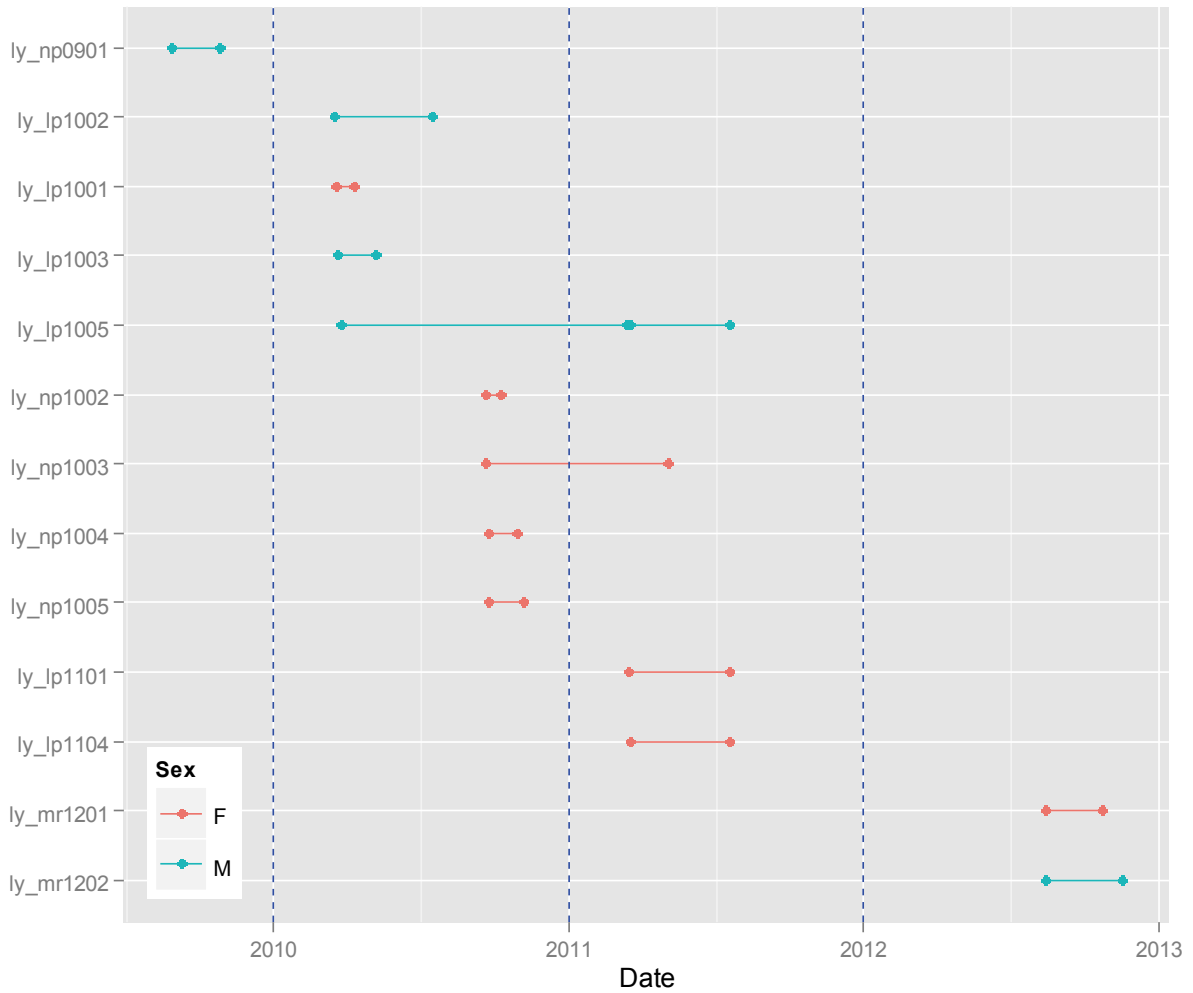
Figure 18. Duration of collaring by sex for 13 lynx (*Lynx canadensis*) in Newfoundland, 2009–2012. Note continuous data were not always available between collar deployment and removal because of battery depletion or collar malfunction. LP = La Poile, MR = Middle Ridge, and NP = Northern Peninsula.

Table 12. Summary of lynx (*Lynx canadensis*) telemetry data in Newfoundland during 2009–2012 showing number of animals collared, number of positional fixes obtained, and mean number of days monitored by study area and sex.

Study area	Sex	Number of animals	Number of fixes	Mean (± SD) monitoring days
	F	3	1,136	90 (62)
La Poile	M	3	1,894	214 (232)
	Total	6	3,030	152 (167)
	F	1	234	71 (-)
Middle Ridge	M	1	308	93 (-)
	Total	2	542	82 (16)

Study area	Sex	Number of animals	Number of fixes	Mean (± SD) monitoring days
Northern Peninsula	F	4	320	80 (98)
	M	1	30	61 (-)
	Total	5	350	76.4 (85)
Sex totals	F	8	1,690	83 (72)
	M	5	2,232	159 (181)
Overall		13	3,922	112 (124)

Home Range Size

Annual home range

Only a single male lynx was tracked long enough to provide an annual home range estimate of 123 km^2.

Seasonal home range

Four lynx provided nine seasonal home range estimates (range: 71–221 km^2) for La Poile and the Northern Peninsula only (Figure 19, Table 13). This limited the statistical analysis to a single non-significant explanatory factor, sex ($F_{1,2} = 0.405$, $p = 0.59$).
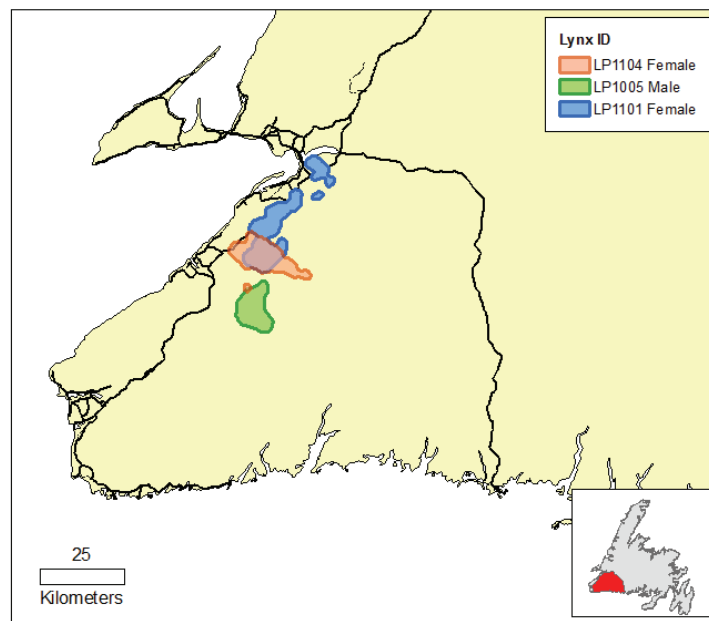
Figure 19. Lynx (*Lynx canadensis*) spring 2011 home ranges in La Poile. Each coloured outline defines the 95% kernel home range of an individual. LP = La Poile.

Table 13. Lynx (*Lynx canadensis*) seasonal home range sizes, number of samples, and number of animals by season, study area, and sex in Newfoundland during 2009–2011.

Study area	Sex	Area (± SD) (km^2) No. samples (No. animals)			
		Spring	Summer	Fall	Winter
La Poile	F	190 (43.8) 2 (2)			
	M	88.5 (24.7) 2 (1)	98.0 (-) 1 (1)	121.0 (-) 1 (1)	111.0 (-) 1 (1)
	Total	139.3 (65.4) 4 (3)	98.0 (-) 1 (1)	121.0 (-) 1 (1)	111.0 (-) 1 (1)
Northern Peninsula	F			75.0 (-) 1 (1)	97.0 (-) 1 (1)
	M				
	Total			75.0 (-) 1 (1)	97.0 (-) 1 (1)
Sex totals	F	190.0 (43.8) 2 (2)		75 (-) 1 (1)	97.0 (-) 1 (1)
	M	88.5 (24.7) 2 (1)	98.0 (-) 1 (1)	121.0 (-) 1 (1)	111.0 (-) 1 (1)
Seasonal totals		139.3 (65.4) 4 (3)	98.0 (-) 1 (1)	90.0 (32.5) 2 (2)	104 (9.9) 2 (2)

Site fidelity

Only a single (male) animal provided enough data to compute site fidelity (range: 0.6–14.3 km; Table 14). For this animal, site fidelity was similar across seasons ($F_{1,110} = 0.282$, $p = 0.75$) ranging from seasonal means of 4.0 to 5.2 km between locations separated by one year.

Table 14. Seasonal site fidelity of a single male lynx (*Lynx canadensis*) in La Poile, Newfoundland, during 2010–2011 as measured by distance between locations one year apart. Smaller distances imply greater site fidelity.

Study area	Sex	Distance (± SD) (km) No. samples (No. animals)			
		Spring	Summer	Fall	Winter
La Poile	M	4.0 (1.9) 60 (1)	5.2 (3.8) 21 (1)		4.8 (2.8) 32 (6)

Daily movement rate

Nine animals provided enough data to compute daily movement rates ($n = 142$, range: 0.6–9.2 km·d^{-1}; Table 15, Figure 20). Movement rates were highest in spring but more similar in other seasons ($F_{3,127} = 4.83$, $p = 0.003$). Movement rates did not differ by sex ($F_{3,3} = 0.33$, $p = 0.61$) or by study area ($F_{2,3} = 1.14$, $p = 0.43$).

Table 15. Seasonal daily movement rates for lynx (*Lynx canadensis*), number of samples, and number of animals by study area and sex in Newfoundland during 2009–2012.

Study area	Sex	Spring	Summer	Fall	Winter
		Movement rate (± SD) (km·d^{-1})			
		No. samples (No. animals)			
La Poile	F	4.3 (2.3) 16 (2)	3.9 (2.7) 6 (2)		3.2 (1.8) 15 (2)
	M	4.0 (0.9) 16 (1)	3.4 (0.8) 18 (2)	3.2 (0.9) 8 (1)	3.2 (1.3) 29 (1)
	Total	4.2 (1.7) 32 (3)	3.5 (1.5) 24 (4)	3.2 (0.9) 8 (1)	3.2 (1.5) 44 (3)
Middle Ridge	F		1.7 (0.7) 8 (1)	2.2 (0.7) 3 (1)	
	M		2.9 (0.5) 8 (1)	2.5 (0.8) 6 (1)	
	Total		2.3 (0.9) 16 (2)	2.4 (0.7) 9 (2)	
Northern Peninsula	F		2.3 (0.2) 2 (2)	1.7 (0.7) 5 (1)	
	M		1.3 (-) 1 (1)	2.1 (-) 1 (1)	
	Total		1.9 (0.6) 3 (3)	1.8 (0.7) 6 (2)	
Sex totals	F	4.3 (2.3) 16 (2)	2.6 (2.0) 16 (5)	1.9 (0.7) 8 (2)	3.2 (1.8) 15 (2)
	M	4.0 (0.9) 16 (1)	3.2 (0.8) 27 (4)	2.9 (0.9) 15 (3)	3.2 (1.3) 29 (1)
Seasonal totals		4.2 (1.7) 32 (3)	2.9 (1.4) 43 (9)	2.5 (0.9) 23 (5)	3.2 (1.5) 44 (3)
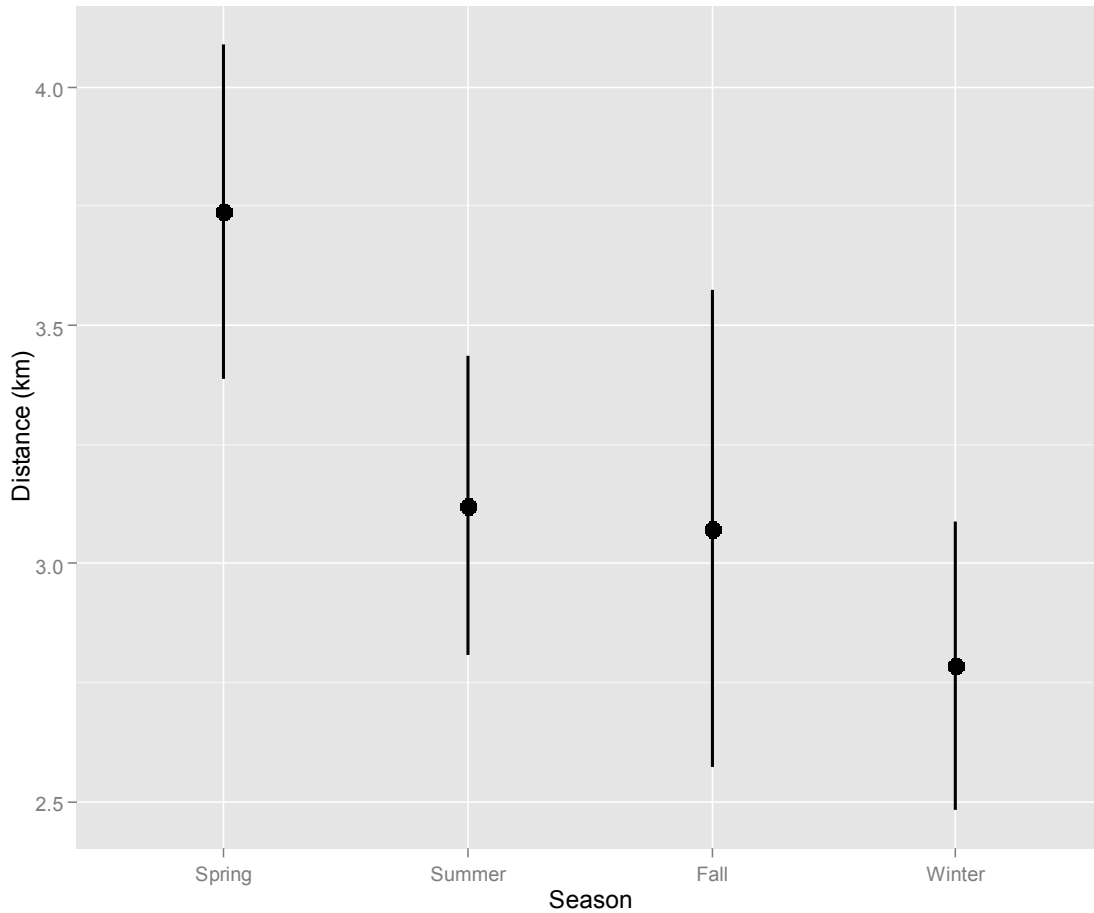
Figure 20. Model predicted (± 95% CI) daily movement rates for lynx (*Lynx canadensis*) in Newfoundland, 2009–2012, showing greatest movement rate in spring, with more consistency among other seasons.

DISCUSSION

This is the first report on spatial ecology for coyotes, bears, and lynx in Newfoundland particularly in the context of their interaction with caribou. Statistically significant results are summarized in Table 16.

Predator home ranges in Newfoundland were large in comparison with those determined for other regions of North America. Male home ranges (both annual and seasonal) exceeded those of females for coyotes and bears but not for lynx, although sample sizes were limited for the latter species. Annual home ranges of transient coyotes were an order of magnitude greater than those of resident coyotes and spanned the breadth of the island, thus involving some of the longest coyote movements ever reported. All predators, except transient coyotes, showed substantial inter-annual site fidelity. Site fidelity was generally greater in female than male coyotes and bears while male movement rates exceeded those of females. Transient coyotes had greater movement rates than resident coyotes during all seasons except fall.

Table 16. Summary of statistically significant results for annual and seasonal home range, site fidelity, and daily movement rate for black bears, coyotes, and lynx in Newfoundland, 2008–2013. LP = La Poile, MR = Middle Ridge, NP = Northern Peninsula, and NS = no significant differences.

	Black bear	Coyote	Lynx
Annual home range	Males > females, but extent of difference depended on study area: LP > MR > NP	Transients > residents	NS
Seasonal home range	Males > females Spring/summer > fall/winter	Transients > residents Residents only: Varied by season: spring: smallest summer and fall: intermediate winter: largest LP > MR > NP	NS
Site fidelity	Females > males Seasonal pattern varied by study area: LP: similar across seasons MR: spring/summer < fall/winter NP: fall/winter < spring/summer	Residents > transients Residents only: Females > males	NS
Daily movement rate	Males > females, especially in spring Varied by season and study area: spring: MR > LP/NP other seasons: study areas are similar	Transients > residents Residents only: Males > females Winter > fall in all study areas Other seasonal patterns varied in complex ways by study area (Figure 17)	Largest in spring, other seasons similar

Home Range Size

Black bear

Annual home range

Black bear annual home range size varied from 54 to 1,347 km^2. Like many other studies, male home ranges (628 ± 585 km^2) were significantly larger than females (181 ± 125 km^2). In the 1990s, smaller female (82 km^2) and male (297 km^2) home ranges were reported for the Serpentine Lake area in western Newfoundland (Dennis et al. 1996), and even smaller (45 km^2) female home ranges were reported in Gros Morne National Park (Mahoney et al. 1997). Note, however, that these Newfoundland home range estimates were based on VHF tracking and should be considered minimal.

Home range sizes for both male and female black bears in other regions of North America were mostly smaller than those we report on here for bears in Newfoundland. Home range sizes for female black bears varied across North America. They were quite small (9–41 km^2) in Pennsylvania, Oklahoma, Tennessee, Washington, Arizona, Florida, North Carolina, and Arkansas (Alt et al. 1977, Bales Lyda et al. 2007, Garshelis and Pelton 1981, Koehler and Pierce 2003, LeCount 1980, McCown et al. 2004, Mitchell and Powell 2007, Smith and Pelton 1990), whereas in Manitoba, Utah and Nevada, and the Gapsé Peninsula (Pacas and Paquet 1994, Beckmann and Berger 2003, Mosnier et al. 2008), they were more similar (173–193 km^2) to Newfoundland females. Likewise, male home ranges were smaller in most of North America (29–173 km^2) but more similar to Newfoundland (303–520 km^2) in the same regions as for females (same locations and references as for females).

As solitary generalists, black bear spatial organization is largely influenced by availability of food resources (Mitchell and Powell 2012). Differences in home range sizes for bears between Newfoundland and the rest of North America and amongst study areas within Newfoundland likely reflect differences in habitat quality (Koehler and Pierce 2003, Mitchell and Powell 2012) and food abundance.

Female home ranges were similar across study areas, but male home ranges were not (Figure 4). They were largest in La Poile, followed by Middle Ridge and then the Northern Peninsula, which may relate to habitat differences among study areas. These factors may also explain the generally smaller home ranges for previous Newfoundland studies in the Serpentine Lake and Gros Morne areas; these areas, along with the Northern Peninsula, are dominated by forest, whereas Middle Ridge and La Poile are bog/fen/barren dominated. Additionally, black bear home range sizes can be influenced by behavioural and demographic factors such as reproductive/social status, competition, hunting patterns, individual food preferences, and for males, the number of estrous females in an area (Koehler and Pierce 2003). Thus, the size and distribution of black bear home ranges do not necessarily reflect forage abundance directly (Mitchell and Powell 2007). Thus, predicting the spatial relationship between bear home ranges via a simple assessment of available resources may be inadequate. The study of bear home ranges in relation to the distribution of resources and in relation to habitat are areas for further research.

Seasonal home range

Home range size varied by season, but in all seasons males had larger home ranges than females (except winter, when no male home ranges were recorded; Table 2, Figure 5). Spring and summer home ranges were larger than fall and winter. This difference may be related to the distribution of berry resources that are highly beneficial to fat accumulation prior to denning. In Newfoundland, berries are broadly distributed so bears may not need to expand their home ranges during the fall berry season. In spring, however, resources might not be as broadly available and more searching may be required. Alternatively, spring ranges might be expanded to facilitate mating (certainly for male black bears) or to prey upon caribou (see movement rates).

Similar to Newfoundland, bears in Arkansas had the smallest home ranges in fall/winter, although summer (8 June – 21 October) home range was larger than spring (1 March – 7 June; Smith and Pelton 1990). Likewise, bears in Pennsylvania had the largest home ranges in June–July (Alt et al. 1980), and in Florida, the smallest home ranges were observed during winter and become progressively larger until peaking during fall (September–December; Wooding and Hardisky 1994).

Home range overlap

Studies elsewhere have reported strong territoriality in low productivity boreal forests (Rogers 1987). However, other authors have found extensive inter- and intra-sexual home range overlap in the boreal forest (Obbard and Kolenosky 1994, Schenk et al. 1998) and elsewhere in North America (Lindzey and Meslow 1977, Garshelis and Pelton 1981, Pacas and Paquet 1994, Wooding and Hardisky 1994, Schenk et al. 1998). It appears that the dynamics of home range overlap result from a complex interaction among population density, food availability, genetic relatedness, and dispersal behaviour (Schenk et al. 1998, Costello et al. 2008), and no universally consistent patterns of home range overlap have emerged to date.

Coyote

Residents versus transients

Consistent with other studies (Litvaitis and Shaw 1980, Holzman et al. 1992, Chamberlain et al. 2000, Kamler and Gipson 2000, Atwood and Weeks 2003, Hidalgo-Mihart et al. 2004, Mosnier et al. 2008, Gehrt et al. 2009, Schrecengost et al. 2009, Boisjoly et al. 2010, Hinton et al. 2012), resident coyotes in Newfoundland occupied defined home ranges for prolonged periods, while transient coyotes made large-scale transient movements between regions. Though not determined in this study, other studies have found transient coyotes were often very young (< 1 year old) or very old animals, or crippled individuals that were unlikely associated with social groups or mated pairings (Roy and Dorrance 1985, Gese et al. 1988). These animals are likely unable to compete in the dominance hierarchy of a resident group (Gese et al. 1988), but may act as a reserve from whence they may be recruited into the breeding population as residents (Camenzind 1978). The categorization of transient and resident individuals is not straightforward and is often subjective and inconsistent among studies. Therefore, inter-study comparisons are difficult, particularly because individuals may periodically switch between behaviour modes (Gese et al. 1988, Kamler and Gipson 2000, Hinton et al. 2012) as they mature or find suitable areas for territory establishment.

Transient coyotes comprised 24.6% of coyotes in this study. Similar percentages have been reported for other regions of North America (Gese et al. 1988, Mills and Knowlton 1991), although the percentage can vary within an area depending upon prey abundance and has reached as high as ~80% during times of prey scarcity in Utah (Mills and Knowlton 1991). Most of the transients observed in this study were males (*n* = 13 of 15), similar to Colorado where 8 of 12 transient coyotes were males (Gese et al. 1988).

Transient coyotes in Newfoundland often demonstrated intermittent localized space use of varying duration (1–12 months) at varying times of year but were characterized by their overall lack of adherence to one area (Figures 10 & 11). Transient coyotes covered large distances in a short time frame, crossing the island in weeks to months. Studies in other areas of North America have also documented long-distance movements of coyotes, although over smaller distances than reported here (e.g., Hinton et al. 2012). In Alberta, coyotes generally made their longest movements in late winter or spring (Roy and Dorrance 1985) and fewer such movements in fall and early winter. Hinton et al. (2012) also recognized the tendency of transient coyotes to periodically establish territorial ranges and called these "biding areas". Biding areas were interpreted as extended foraging efforts or pre-settlement habitat assessment (Hinton et al. 2012).

Annual home range

Annual home range estimates for resident coyotes in Newfoundland were comparable with mean home ranges of coyotes reported in the Gaspé region, where coyotes were also recent colonizers (Mosnier et al. 2008, Boisjoly et al. 2010), but were much larger than those reported elsewhere in other parts of North America. Home ranges of less than 10 km^2 have been reported in British Columbia (males; Atkinson and Shackleton 1991 in Feldhamer et al. 2003), Alberta (Bowen 1982, Roy and Dorrance 1985), Georgia (males; Holzman et al. 1992), Indiana (Atwood et al. 2004), Kansas (Kamler and Gipson 2000), Texas (Andelt 1995), New Mexico (Windberg et al. 1997), and Mississippi (females; Chamberlain et al. 2000), while home ranges of 10–20 km^2 were reported in British Columbia (females; Atkinson and Shackleton 1991), Mississippi (males; Chamberlain et al. 2000), and Colorado (Gese et al. 1990). Home ranges between 20–138 km^2 were found in Georgia for female coyotes (27.9 km^2; Holzman et al. 1992) and for males and females in Oklahoma, Arizona, Idaho, Utah, Minnesota, and Nebraska (Litvaitis and Shaw 1980 and references therein).

Similar to bears, large home ranges may suggest poor food availability since home range size decreases with decreased latitude and increased food abundance (Gomper and Gittleman 1991, Mills and Knowlton 1991, Patterson and Messier 2001, Hidalgo-Mihart et al. 2004). Food resources in Newfoundland likely are a function of the lower productivity of the boreal forest relative to the more temperate ecosystems and agriculturally dominated areas found in the above studies. Young et al. (2008) found that coyotes supplemented with a high quality food source increased their home range size once supplementation ceased. Alternatively, though coyotes are found throughout Newfoundland, they are relatively recent colonizers and densities may still be increasing. If this is true, available habitat may not yet be fully exploited allowing for large home range sizes. Given their reproductive capacity and vagility and the fact that they have been in Newfoundland for at least three decades, we suspect this is not the case.

Mean home ranges sizes of transient coyotes were almost five times larger than those of resident coyotes and one transient male had an annual home range of 2,529 km^2, nearly seven times larger than the mean for resident coyotes (Table 6). McGrath et al. (2009) also reported

home range estimates for transient Newfoundland coyotes ranging from 1,105 to 3,015 km^2, and transient coyotes of the Gaspé region had comparable ranges (Boisjoly et al. 2010). Likewise, home ranges for transient coyotes were an order of magnitude larger than those for resident coyotes in other areas (Gese et al. 1988, Andelt 1995, Kamler and Gipson 2000, Mosnier et al. 2008, Gehrt et al. 2009). The reasons for the large home range sizes for transient coyotes in Newfoundland in comparison with the rest of North America are likely similar to those for the large home range sizes for resident coyotes.

While many resident female annual home ranges (mean: 175.2 km^2) were smaller than those for males (mean: 310.3 km^2), variation was large and there was no statistically significant difference between the sexes. McGrath et al. (2009) reported average home range sizes in Newfoundland of 258 and 232 km^2 for resident males and females, respectively. Smaller female home ranges have been reported in other regions of North America (Andelt 1995, Mosnier et al. 2008) but similar male and female home range sizes were also common (Laundré and Keller 1984, Gese et al. 1988, Holzman et al. 1992, Chamberlain et al. 2000). Other important influences on home range size were age, season, and habitat type (Laundré and Keller 1984, Gese et al. 1988, Holzman et al. 1992, Atwood and Weeks 2003). The variability in annual home range sizes could therefore be due to differential responses of males and females to habitat and environmental conditions in each area or to unknown variation in sample populations among study areas.

Coyotes on ice

At least two coyotes, both males, spent prolonged periods traveling over sea ice (Figure 11). For example, one animal spent nearly 3 weeks on the ice during February 2011 and traveled more than 180 km, moving from the tip of the Northern Peninsula and coming ashore near Baie Verte. At least three other animals in the Northern Peninsula region traveled shorter distances off the coast. Forty percent of coyotes in this study made use of coastal areas to a varying extent and duration, and it is possible that more coyotes made unobserved short excursions onto sea ice. It is highly likely that ventures onto the sea ice represent foraging excursions for pupping seals or seabirds thereby directly integrating marine resources into the coyote's diet (Rose and Polis 1998). Evidence of prolonged sea ice excursions provide support for the generally accepted theory that coyotes colonized the island of Newfoundland from mainland Canada using the sea ice as a bridge.

Seasonal home range

Resident coyote home ranges differed by season; spring ranges were smaller than summer and fall, which were generally smaller than winter ranges (Figure 13). Food is presumably more limited during winter and larger home ranges have been associated with seasonal declines in food availability (Bekoff and Wells 1986, Mills and Knowlton 1991, Holzman et al. 1992, but see Andelt 1995, Chamberlain et al. 2000, Hidalgo-Mihart et al. 2004). Males had larger home ranges than females in all seasons. Similar to bears, seasonal home range size of resident coyotes varied by study area with home ranges in La Poile being larger than those in Middle Ridge, which were larger than those in the Northern Peninsula. This could imply differential food resources in each study area and suggests the possibility of a similar underlying mechanism across species. Alternatively, for coyotes, this could result from the unbalanced sex ratio of our samples with a prevalence of males in La Poile and females in the Northern Peninsula (Table 7).

45

Transient coyotes had larger home ranges than resident coyotes in all seasons except fall (Figure 13). Similarly, Bekoff and Wells (1986) found that fall home ranges were smallest for both resident and transient coyotes and suggested this was due to increased prey abundance in their study area at that time.

Home range overlap

With the exception of mated pairs, resident coyotes displayed little or no overlap between adjacent home ranges, whereas transient coyote home ranges overlapped considerably with those of resident coyotes (Figures 14 & 15). This pattern is consistent with coyotes in other regions of North America (Bowen 1982, Roy and Dorrance 1985, Gese et al. 1988, Andelt 1995, Chamberlain et al. 2000, Kamler and Gipson 2000, Patterson and Messier 2001, Atwood and Weeks 2003, Schrecengost et al. 2009). However, these results must be cautiously interpreted since unobserved range overlap may have occurred between our study animals and uncollared coyotes. Schrecengost et al. (2009) reported only 22.4% ± 6.7% home range overlap between unrelated individuals but 72.9% ± 5.6% range overlap between members of mated pairs. The extent of home range overlap between individuals from different pairs/packs may be related to the abundance of food and cover. In urban/suburban areas where food was plentiful, coyotes in Indiana overlapped to a much greater extent than those in agricultural areas (Atwood and Weeks 2003). However, coyote packs in forested regions of Nova Scotia maintained territories even during high food abundance, which Patterson and Messier (2001) speculated was the result of coyotes protecting food resources against future shortages.

Lynx

For lynx, only one annual home range (122 km^2) could be calculated during our study. In addition, seasonal ($n = 9$) ranges were recorded for four individuals (mean range: 111.5 km^2; Table 13). These estimates are higher than those reported for lynx in Maine (Vashon et al. 2008), Washington (Koehler 1990), Nova Scotia (Parker et al. 1983), and Alberta (Brand et al. 1976), but are similar to home ranges reported for lynx in the Yukon (Slough and Mowat 1996), Minnesota (Mech 1980, Burdett et al. 2007), Alaska (Bailey et al. 1986), and Manitoba (Carbyn and Patriquin 1983). Large home range sizes have been reported for lynx populations during the cyclic population low of snowshoe hares (Slough and Mowat 1996), for marginal habitats (Carbyn and Patriquin 1983), and for heavily exploited lynx populations (Mech 1980, Bailey et al. 1986). Snowshoe hares in Newfoundland were at a low in their population cycle during this study (Reynolds et al. 2011), which may help explain the large home range sizes observed.

The few lynx home ranges described here were clustered and some overlapped (Figure 19). Lynx are thought to behave as solitary and territorial animals, tolerating little overlap of home ranges, though clustering of home ranges has been noted in regions of high hare densities (Bergerud 1971, Brand et al. 1976, Carbyn and Patriquin 1983). Additionally, extensive video footage from our trapping efforts suggests that multiple lynx may visit a single baited trap and that individuals at a trap site may respond either prosocially or antagonistically to each other (SDSS, unpublished data).

No differences in home range sizes were observed between the sexes in this study (Table 13), though other studies have shown female lynx to have smaller home ranges than males (Mech 1980, Bailey et al. 1986, Koehler 1990, Burdett et al. 2007, Vashon et al. 2008). These sex differences were most commonly explained by female association with den sites,

accompaniment by kittens (Vashon et al. 2008), or reproductive efforts (Burdett et al. 2007). Sex differences in lynx distributions may be important since males are thought to establish home ranges based on female distribution (Burdett et al. 2007).

Site Fidelity

Black bear

On average, bears were found to be 11.2 km from their position on the same date in the previous year. Female black bears displayed greater site fidelity than males (Figure 7A), which is common in this species (Schwartz and Franzmann 1992, Costello 2010, Rayl 2012). Female bear fitness is most strongly influenced by nutritional status and food availability, and site fidelity allows female bears to efficiently exploit resources in a familiar area (Costello 2010). In contrast, male space use, at least during mating season, is most strongly influenced by searching for multiple mates whose territories overlap their own (Gittleman and Harvey 1982, MacDonald 1983, Sandell 1989, Mitchell and Powell 2007). Additionally, young bears typically disperse and may wander for several years (i.e., displaying low site fidelity) before establishing a territory (Costello 2010).

Site fidelity varied by season and study area (Figure 7B). Excluding winter denning, bears in Middle Ridge displayed less site fidelity during summer than in fall, which is consistent with smaller fall home ranges (compared with other seasons, see above) for Newfoundland bears in general. However, in the Northern Peninsula, bears displayed greater fidelity during spring and summer than in fall, and in La Poile, site fidelity was similar during these three seasons.

Theory predicts that as variability in spatiotemporal resource availability increases, fidelity should decrease (Wiens 1976). The variation we observed in relative seasonal fidelity among study areas implies variation in the predictability of seasonal resources of interest (i.e., food and/or mates depending on the season) in each area. Marked spring and summer site fidelity is consistent with the idea that (some) Newfoundland bears return to predictable calving grounds at this time (Rayl 2012), while strong fidelity in fall is consistent with the exploitation of predictable berry crops (Obbard and Kolenosky 1994). Lower fall fidelity could be associated with wider dispersal to search for moose and caribou gut piles from harvested animals or baits (in areas of outfitter activity). Further elucidation of the relative importance of factors driving differential seasonal site fidelity among study areas would require more research.

Coyote

Resident coyotes demonstrated far greater fidelity to their home ranges between years than transient coyotes. On average, resident coyotes were found to be 6.1 km away from their recorded locations on the same date in the previous year, whereas transient coyotes showed little annual consistency in where they spent time with a mean distance between inter-annual positions of 199.1 km (Table 8, Figure 16B). Female coyotes displayed greater site fidelity than males in all seasons. Given that females have smaller home ranges than males (see above), it follows that the distance between inter-annual positions would also be smaller.

Coyotes have been shown to remain faithful to a site although space use varied temporally within site boundaries (Kitchen et al. 2000, Patterson and Messier 2001). However, the extent of site fidelity may depend on local population stability; coyotes altered their space use when neighboring territories became vacant because of coyote removal (Young et al. 2008).

47

Coyote fidelity also likely depends upon social status, with high-ranking individuals remaining faithful to the site while low-ranking individuals disperse (Gese et al. 1996).

The marked difference in site fidelity between transient and territorial coyotes offers an alternate approach to characterizing these behaviour modes as opposed to the maximal distance between points method used in this study.

Lynx

One lynx in this study was assessed for site fidelity and remained a mean of 4.19 km from recorded locations on the same date of the previous year. This is broadly comparable with the shift in home-range centroids of up to *ca.* 2.5 km between years for lynx in Maine (Vashon et al. 2008). Strong lynx home range fidelity has also been shown in the Northwest Territories (Poole 1994, 1995) and Washington (Koehler 1990).

Daily Movement Rate

Black bear

Daily mean movement rates of bears (0–11.7 km·d^{-1}) were similar to those in the Serpentine Lake area of Newfoundland (11.3 and 15 km·d^{-1}; Dennis et al. 1996) and overlapped broadly with those of bears in Alberta (1.7 km·d^{-1}; Young and Ruff 1982), the southern Appalachians (1–11 km·d^{-1}; Garshelis et al. 1983), Idaho (0.9–1.7 km·d^{-1}; Amstrup and Beecham 1976), and Minnesota (1.6–2.7 km·d^{-1}; Rogers 1977 in Young and Ruff 1982). In this study, the greatest movement rate occurred in spring, and movement rates of males exceeded those of females, particularly during spring (Figure 8). In Gros Morne National Park in the 1990s, movement rates were greatest in summer followed by spring and fall (Mahoney et al. 1997). In general, greater movement rates in spring have been reported for black bear populations in a wide range of North American locations. These increased movement rates may be due to lower food availability during the early post-winter period (Young and Ruff 1982) and have been hypothesized to increase black bear encounters with neonate caribou calves in Newfoundland (Rayl 2012). Male bears likely move farther during spring in search of multiple mates (Amstrup and Beecham 1976) or because of agonistic encounters between rival males (Young and Ruff 1982). Thus, the overall decrease in movement rate and the decreasing difference between males and females from spring through fall likely results from increased food availability in fall and the termination of the breeding season (Young and Ruff 1982).

Seasonal movement rates were similar across study areas except during spring when rates were significantly greater in Middle Ridge (Figure 8). This could reflect poorer (or more dispersed) food availability in Middle Ridge or longer deliberate migrations by black bears to the Middle Ridge caribou calving grounds preceding parturition (Rayl 2012).

Coyote

Resident coyotes had an overall daily movement rate of 4.1 ± 4.0 km·d^{-1} (range: 0.1–37.0 km·d^{-1}). Resident Newfoundland coyote movement rates were broadly similar to those from studies reporting daily (1.7 km·d^{-1}, Oklahoma, Litvaitis and Shaw 1980; 1.0–2.4 km·d^{-1}, Alberta, Roy and Dorrance 1985; 8 km·d^{-1}, Texas , Andelt 1995; 2.3 km·d^{-1}, North Carolina, Hinton et al. 2012) or hourly (0.4–0.7 km·h^{-1}, Mississippi, Chamberlain et al. 2000; < 1.0–2.8 km·h^{-1},

Wyoming, Bekoff and Wells 1986; 0.2–0.5 km·h^{-1}, Georgia, Holzman et al. 1992) movement rates. Likewise, Newfoundland transient movement rates (4.9 ± 4.3 km·d^{-1}, range: 0.03–29.4 km·d^{-1}) were similar to those in North Carolina (2.8–6.7 km·d^{-1}, Hinton et al. 2012).

Males had greater daily movement rates than females in all seasons (Figure 17), contrary to many studies (Litvaitis and Shaw 1980, Andelt 1995). For example, Sumner et al. (1984) found greater nightly movement rates for females in all seasons, and Chamberlain et al. (2000) and Holzman et al. (1992) reported greater movement rates for females during pup-rearing. Chamberlain et al. (2000) speculated that greater female movement rates may be due to a greater need to provision food for growing pups (even though both males and females provide food). The cause of greater male movement rates in Newfoundland remains unclear.

The relative seasonal pattern of daily movement rates varied by study area, although winter movement rates were greater than those during fall in all areas. Likewise, nightly movements of coyotes in Mississippi were largest in winter and smallest in fall, which Sumner et al. (1984) hypothesized was either due to changes in food habits (i.e., switching to a more locally abundant food source in fall) or due to increased movements for mate selection and pair formation during winter.

Transient coyotes displayed greater movement rates than resident coyotes in all seasons except fall (Figure 17C). Very few studies have focused on daily movement rates of transient coyotes, and we are unaware of any study directly comparing resident versus transient movement rates, although Hinton et al. (2012) observed one coyote that switched from transient to resident and had a greater movement rate as a transient.

Although statistically different, daily movement rates were numerically similar between residents and transients (Table 11), especially in light of their vastly different home range sizes (Table 7). This similarity may reflect a tendency for coyotes, regardless of behaviour mode, to cover a similar amount of ground daily. The difference in behaviour between resident and transient coyotes is thus not in the amount of ground covered daily but how it is covered (i.e., with residents remaining within a small defined home range and transients dispersing widely).

The Newfoundland transient coyotes' reduced movement rates in fall could be due to abundant localized food sources (Mills and Knowlton 1991) and may be influenced by hunting activity (gut piles in particular). Reduced movement rates may be linked to a greater propensity to assess potential permanent home range areas in the fall (Hinton et al. 2012). Further research on a larger number of animals would help to elucidate underlying mechanisms.

Lynx

Movement rates of lynx in this study averaged 3.18 km·d^{-1}, with no difference detected between the sexes or among study areas, although sample size was small for all comparisons. Spring movements were greatest while winter movements were smallest (Figure 20). Similarly, Poole (1994) found daily movements of lynx to be variable between seasons in some years, but not between sex or year. Also, Parker et al. (1983) found lynx movements in Nova Scotia to be highest in the summer and lowest in the winter.

Few lynx data were available for this report because of the inability to relocate animals' collar signals from the air (for collar download), which was likely due to the dense forest cover in areas favoured by Newfoundland lynx and/or premature (battery) failure. This could be mitigated by more intense (yet expensive) relocation and remote download efforts or by the future availability of satellite downloadable collars whose transmit duty cycle is adapted for the heavy forest cover.

Conclusions, Applications, and Future Direction

The main objective of this study was to better understand the spatial ecology of bears, coyotes, and lynx with specific focus on home range size, site fidelity, and movement rates in order that this information might improve the understanding of both predation and caribou ecology and management. Predators use space at different scales at different times of the year for a variety of reasons including resource acquisition, breeding, and birthing. Changes in space use may precede observations of demographic or habitat changes (e.g., Schaefer and Wilson 2002, Faille et al. 2010) and may thereby contribute to ecosystem management by providing an early warning of such changes.

Understanding predator ecology and space use has important implications for the integrated management of predators and caribou. For example, SDSS tested the effect of diversionary feeding of black bears (2010–2011) and removal of coyotes (2012–2013; Gullage et al., in prep.) on calf survival. One the most significant findings relative to predator management efforts is the long-distance movement of transient coyotes. The ability of this canid to cross Newfoundland in a few weeks suggests that any area depopulated by directed management action such as predator removal could be quickly recolonized. In addition, the home range size of bears and coyotes in this study are amongst the largest reported in North America. Such large home ranges increase the likelihood of home range overlap between caribou and predators, although the low density of predators (Fifield and Lewis 2013) may reduce the likelihood of encounter. On account of large range sizes, the home ranges of many predators will partially overlap any management or removal areas, necessitating a wide buffer around these areas to improve the efficacy of the removal and the ability to measure its impact.

However, for any management action, but especially for predator removal, several important quantities have not been measured that are required to assess long-term efficacy. First, it is not clear how long the effect of a removal of coyotes and bears would last because of unknown recolonization rates. Second, regarding the overlap of territories of individual predators, it is not know if removing a single predator (or mated pair) would create a predator-free gap where predation on caribou is minimal. Or do predators in adjacent areas move in to fill the gap? Third, what factors influence the behavioral status (resident versus transient) of coyotes? The recolonization ability of these animals is potentially great but it is not clear what demographic, morphological, or behavioural factors influence their behavioural mode.

This study has been the first to outline patterns of predator space use in relation to a number of fundamental variables (i.e. sex, season, study area, and behavior mode) and provides a foundation to inform our understanding of both their observed predation on caribou and implications and utility of predator management strategies.

ACKNOWLEDGMENTS

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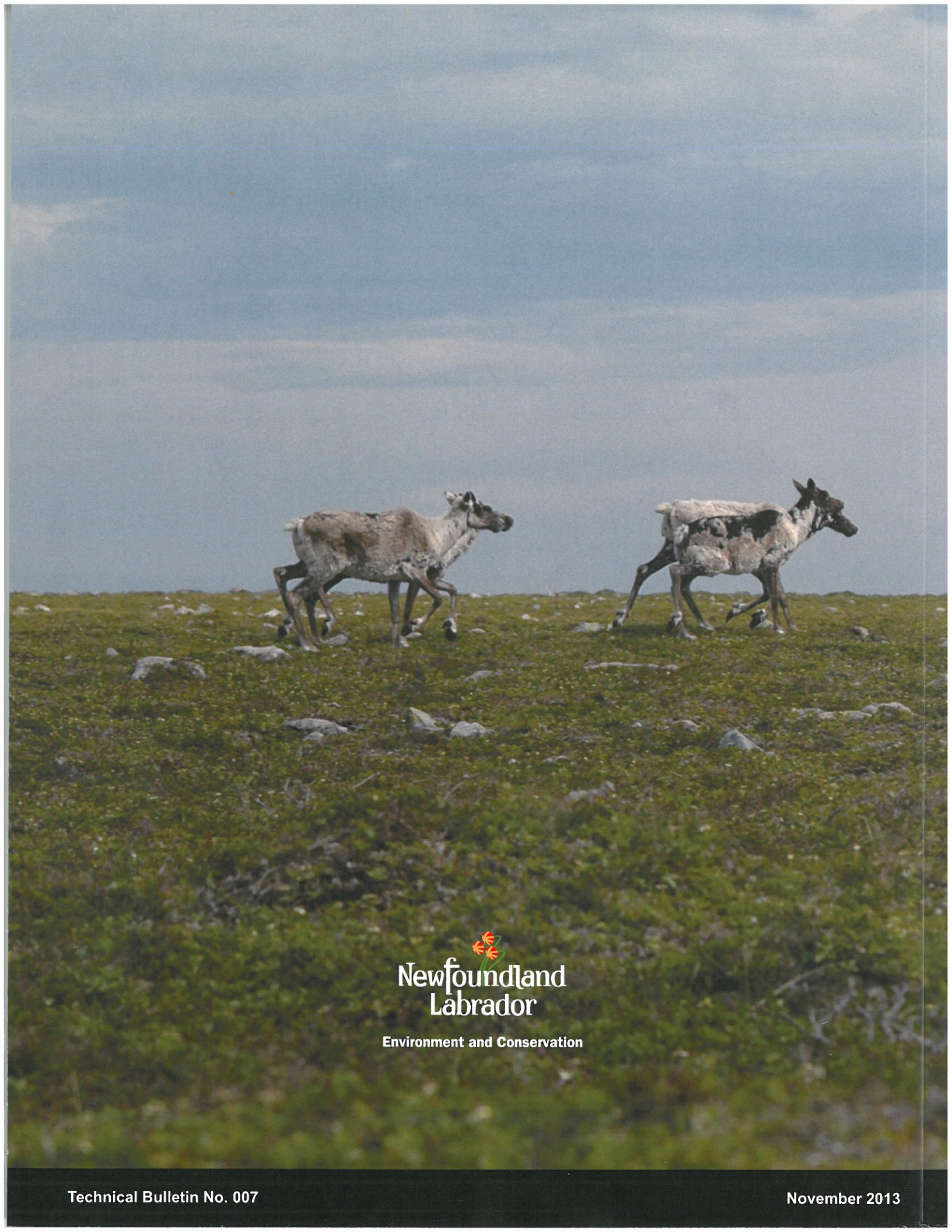
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