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Drawing lines: Spatial behaviours reveal two ecotypes of woodland caribou



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ABSTRACT

Ecotypes offer an essential framework for conservation and ecological understanding, but their identification can be problematic. These challenges are exemplified by the sedentary and migratory ecotypes of woodland caribou (*Rangifer tarandus caribou*). In Ontario, Canada, reliable discrimination based on morphology, pelage, or genetics has been unsuccessful. We tested the discriminatory power of locational and movement metrics as candidate indicators of discrete behaviours for 132 GPS-tracked female caribou. We assigned each animal to an ecotype each year using two variables which demonstrated the strongest bi-modality and the best discriminatory power: percent of calving season locations within the Hudson Bay Lowland and mean distance to treeline during calving season. The analysis revealed two distinct modes. None of 101 caribou tracked for more than 1 year switched behaviours, implying the distinction may be permanent. Although there was no significant difference in morphology between ecotypes, mean aggregation metrics and calving dates were significantly different. Geographic distribution of thes ecotypes showed substantial range overlap, particularly during winter, which presents challenges for conservation of the sedentary ecotype, a threatened designatable unit under federal and provincial legislation. Woodland caribou — with its cryptic ecotypes, discernible from differences in spatial behaviour — illustrate the importance of this type of analysis for identifying significant units for protection, understanding habitat relationships, and delineating ranges for habitat protection.

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1. Introduction

Classification and taxonomy are fundamental to biological understanding and conservation. Little consensus has emerged, however, on the numerous grouping concepts and terminology below the species level (Cronin, 2006). At the same time, the proliferation of approaches to intraspecific classification tends to reflect – and to influence – contemporary social and political concerns for conservation. Endangered species legislation generally recognizes that species-level specifications do not offer adequate resolution for conserving the ecological value for which the legislation is intended, which makes the species concept a blunt tool for conservation purposes (Ceballos and Ehrlich, 2002).

To deal with this shortcoming, a variety of concepts and terms have emerged: subspecies, sub-population (Wells and Richmond, 1995), distinct population segments (US Fish and Wildlife Service, 1973), evolutionarily significant units (Ryder, 1986), evolutionary units (Committee on scientific issues in the Endangered Species Act, 1995), and designatable units (DUs; COSEWIC, Committee on the Status of Wildlife in Canada, 2010). Recently, Morrison (2012) underscored the utility of subspecies and ecotypes. Conclusions about the relationships between demography and habitat, for example, may differ when ecotypes are taken into account, as opposed to when observations are pooled for the whole species. Such contradictory or counter-intuitive inferences under different groupings of observations are known as Simpson's paradox, an analytical pitfall, which can arise when critical classification variables are omitted from analyses (Clark et al., 2011; Kievit et al., 2013). Ecotypes reflect fundamental differences in life history characters; ecotype characteristics may signify emergent adaptive responses to environmental variation and, therefore, underlying traits of evolutionary significance. Morrison (2012) argued that recognizing intra-species structure and geographic ranges are precursors of ecological research. Identifying ecotypes may provide a foundation for stronger inference, better understanding, and more effective conservation.

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Drawing lines to delineate geographic ranges has profound practical ramifications. In Canada, for example, the bases for identifying designatable conservation units are discreteness and character significance (COSEWIC, Committee on the Status of Wildlife in Canada, 2010; Green, 2005; Mee et al., 2015). Elements of these two criteria can include genetic distinctiveness, dissimilar morphology, differing movement behaviours, geographic range separation, phylogenetic divergence, local adaptations to ecological settings, and the degree to which the unit is irreplaceable or the only natural occurrence (COSEWIC, Committee on the Status of Wildlife in Canada, 2010). Although caribou, "reindeer" in Eurasia, (Rangifer tarandus) represent one circumpolar species, biologists have found utility in the ecotype concept. Ecotype is a classification of organisms based on differences in morphology, physiology, behaviour or genetics, which have arisen from local adaptation to heterogeneous environmental conditions (Morrison, 2012). In North America three caribou ecotypes have been identified: migratory tundra, boreal forest (sedentary) and mountain (Hummel and Ray, 2008).

Within the woodland caribou subspecies (*R. tarandus caribou*), which is the focus of this research, two ecotype designations, migratory and sedentary, have been applied (Hummel and Ray, 2008). The distinction stems from the differences in the strategies by females at parturition to minimize predation (Bergerud, 1988). Similar migratoryresidency dichotomies have been recognized for killer whales (Orcinus orca, Morin et al., 2006), bottlenose dolphins (Tursiops truncatus, Torres et al., 2003), and grey wolves (Canis lupus, Schweizer et al., 2015). The migratory-sedentary behaviour is not always evident as a dichotomy, and some species exhibit behaviours on a continuum that includes partial migration (Yellowstone pronghorn, Antilocapra americana, White et al., 2007; roe deer (Capreolus capreolus, Cagnacci et al., 2011). Differences may be subtle and difficult to detect and some population behaviours are best classified by fuzzy classification methods (Pillar, 1999; Schaefer and Wilson, 2002). It is often pivotal to ecological research and biological conservation to determine whether such behaviours are more accurately represented by a continuum or by discrete classes.

Caribou serve as an excellent test case for the identification of DUs and for range mapping. In Ontario, Canada, this animal is represented by one subspecies (R. tarandus caribou), but within-subspecies differences have long been recognized. Simkin (1965) observed two migration and movement behaviours and, at least since Darby et al. (1989), two ecotypes have been identified: a sedentary ecotype, also referred to as "forest-dwelling" or "boreal forest" ecotype; and a migratory ecotype, also called "forest-tundra" ecotype. At calving, females of the sedentary ecotype "space out" from other parturient females and make themselves rare in the midst of predators (Bergerud, 1985; Bergerud et al., 1990). Migratory females, on the other hand, move northward beyond the treeline onto the tundra, and "space away" from areas of higher wolf density. These distinctions translate into demographic differences, where the population growth of the sedentary ecotype is limited by predation and the migratory ecotype population is often limited by forage availability (Bergerud, 1996, 1985; Bergerud et al., 2008; Couturier et al., 2010). Moreover, the sedentary ecotype ("boreal" population) is considered a DU and listed as threatened, provincially and nationally; the "eastern migratory" ecotype, another DU, is not similarly protected (Festa-Bianchet et al., 2011). The two ecotypes have not been readily, nor reliably, distinguishable morphologically (Couturier et al., 2010), except on the basis of male antler conformation (Butler, 1986 in Bergerud et al., 2008). Genetic diversity and structuring has not proven to be a strong discriminating criteria for these ecotypes (COSEWIC, Committee on the Status of Wildlife in Canada, 2011; McQuade-Smith, 2009), although some low, but significant, differentiation has been reported in Labrador-Quebec herds (Boulet et al., 2007).

Here, we capitalized on a multi-year, broad-scale dataset to test the utility of spatial behaviours as discriminators of ecotypes of woodland caribou. Our data were collected from 132 female caribou, livecaptured across the breadth of northern Ontario, Canada; most animals were monitored for 2 years or more. Consistent with the ecotypic descriptions (Bergerud, 1988, Bergerud et al., 2008), we anticipated that migratory and sedentary females would be distinguishable, in particular, by their calving locations relative to treeline. We also tested the discriminatory power of other movement and location metrics. Based on the predation minimization strategies described, we predicted that migratory caribou, compared to sedentary caribou, would have longer path lengths, larger, less compact and more elongated home ranges and more calving season animal locations in the more northerly Hudson Bay lowlands, closer to treeline. After choosing variables to assign animals to classes, we reported on multi-annual consistency of the classification and assessed other characteristics that might be expected to vary by ecotype - i.e., morphology, calving phenology and gregariousness (Bergerud et al., 2008; Couturier et al., 2010). Finally, given the importance of geographic units to conservation, we mapped annual and seasonal ranges of each ecotype, determined their degree of overlap, and discussed the implications for conservation.

2. Methods

2.1. Study area

Our study took place in Ontario, Canada, north of the area of commercial forest management (Fig. 1) and included a small portion of northeastern Manitoba, where caribou spent at least part of the year. The study area was defined by the ranges of animals collared for the Far North Caribou Project, undertaken in support of community-based land use and resource planning (Berglund et al., 2014). The area included portions of two very distinct and different ecological regions: the Hudson Plains and the Boreal Shield ecozones (Environment Canada, Agriculture and Agri-Food Canada, 2012, Fig. 1). The Hudson Plains ecozone was characterized by low elevation, with beach ridges surrounded by silt and clay-rich soils subject to permafrost. It was a patchwork of wetlands with dominant vegetation types including Cyperaceae, Sphagnum, shrubs (such as Betula nana and Empetrum nigrum), Picea, Larix laricina, Abies balsamea, and Populus). Mean summer and winter temperatures were 14 °C and -24 °C respectively (Environment Canada, Agriculture and Agri-Food Canada, 2012). The Boreal Shield ecozone was underlain by the Precambrian shield. Frequent forest fires shaped the vegetation; it was mainly forest, interspersed with lakes and wetlands. Dominant vegetation included Picea, Pinus banksiana, Abies balsamea, and Populus. Mean summer and winter temperatures were 17 °C and -15 °C respectively (Environment Canada, Agriculture and Agri-Food Canada, 2012).

2.2. Observations and variables

The data were collected from 132 female caribou, which were captured, measured, and fitted with GPS collars (model TGW-4680 from Telonics Inc., Mesa, AZ, USA; models GPS 7000MA and IridiumTrackM 3D from Lotek Wireless Inc., Newmarket, ON, Canada). The captures were made in late February and early March, 2009, 2010 and 2011 across northern Ontario (Fig. 1). The location (fix) interval was 25 h (Berglund et al., 2014; Ministry of Natural Resources and Forestry, 2014). The collars collected data for up to three years; data for calving season analyses were available for 31 caribou for only one year, 32 caribou for 2 years and 69 caribou for 3 years. Morphological measurements made at the time of capture included chest girth and hind foot length.

Because caribou ecotypes are hypothesised to minimize predation at calving (Bergerud, 1988), we analysed movement and locations from calving and early post-calving. We identified parturition by the slowing of movement during the spring. For sedentary caribou, Ferguson and Elkie (2004) found a drop to 1.1 km/day (45.8 m/h) for approximately 3 days indicative of calving. DeMars et al. (2013)



Fig. 1. Study area showing woodland caribou capture locations, and capture locality names, ecozones, ecoregions and the tundra-taiga treeline.

estimated a threshold of 15.3 m/h for a 3-day moving average. We found movements <500 m/25 h (20 m/h) for \geq 3 days a consistent threshold (Wilson, 2013). These inferences provided earliest (1 May) and latest (9 June) calving dates, which we used to define a standard 40-day calving season, including early post-calving, for all years. For analysis of seasonal ranges by ecotype, we defined four other 40-day seasons, comparable to the length of the inferred calving season: breeding (9 September–19 October), which preceded the calving season by a 234 day gestation period (Bergerud et al., 2008), early winter (1 January–9 February), late winter (10-February–21 March) and summer (23 July–31 August).

We hypothesised that path length, range area and range perimeter during calving season would be smaller for sedentary compared to migratory caribou and that ranges of the sedentary animals would be more compact and less elongated than migratory caribou. We computed path length for each animal within each calving season as the sum of the distances between successive animal locations during calving season. We delineated seasonal range polygons as minimum convex polygons (MCPs) for each animal within each calving season and computed their areas and perimeters. As indices of shape and elongation in particular, we used the simple perimeter to area ratio (km/km²) and the ratio of MCP perimeter and the perimeter of a circle having the same area as the MCP (km/km) (Moser et al., 2002). Based on Bergerud's (1996, 1988) observations and definitions of ecotypes, migratory caribou move north of treeline at calving to areas of lower wolf density. In Ontario, however, the migratory southern Hudson Bay caribou population, constrained by the Hudson Bay coastline, has only 5% of its annual range north of treeline (Gunn et al., 2012; Newton et al., 2015). The Hudson Bay Lowland, in contrast to the boreal forest to the south, has lower wolf densities (Berglund et al., 2014; Patterson, 2009; Poley et al., 2014). Therefore, we also estimated the percent of calving season animal locations within (a) the narrow coastal ecoregion at the Hudson Bay coast, (b) the Hudson Bay Lowland lying north and northeast of the boreal shield, and (c) the whole of the

Table 1

Candidate discriminating variables for identifying bi-modality and discriminating ecotypes of caribou and their predicted relationships. All variables were computed from calving season locations.

Variable type	Variable	Predicted relationship between means
Movement, home range size and shape	Path length: the sum of the distances (km) between successive animal locations. MCP area: area of 100% minimum convex polygon (MCP) (km ²) for calving season animal locations. MCP perimeter (km) MCP edge to area: ratio of MCP perimeter to MCP area MCP shape: ratio of MCP perimeter to circumference of circle having same area as MCP	Sedentary < migratory Sedentary < migratory Sedentary < migratory Sedentary < migratory Sedentary < migratory
Location	Percent calving locations in CstHBL (Coastal Hudson Bay Lowland ecoregion) Percent calving locations in HBL (Coastal Hudson Bay Lowland and the Hudson Bay Lowland ecoregions) Percent calving locations in HB-JBL (Hudson Plains Ecozone, which includes the James Bay Lowland) Distance to Treeline: mean distance (km) to the northern boundary of the taiga-tundra ecotone for calving locations; locations north of treeline were assigned negative values.	Sedentary < migratory Sedentary < migratory Sedentary < migratory Sedentary > migratory

lowland, which encompasses the James Bay Lowland and is also known as the Hudson Plain ecozone. Given that these areas might serve as refugia from predation, we anticipated a much lower percentage of calving season locations for sedentary than migratory caribou in these regions.

For each animal in each calving season we computed indices of movement and location as candidate discriminatory variables (Table 1). We used maps from the national ecological framework (Environment Canada, Agriculture and Agri-Food Canada, 2012) to assign each caribou location to an ecological region. We digitized the northern boundary of the taiga-tundra ecotone dataset (Montesano et al., 2009; Ranson et al., 2011) as treeline and computed its distance to every animal location. Locations north of treeline were assigned negative distances. This distribution of distances to treeline was positively skewed, as were the distributions of other movement and range data. Therefore we applied a natural logarithmic transformation to all except the percentage variables. As a measure of aggregation behaviour, we computed distances from each caribou location to its first to fifth nearest collared animal within a \pm 12 h temporal window. We computed the mean of five nearest-neighbour distances for each caribou during each calving season.

2.3. Analysis

2.3.1. Ecotype discrimination

Recognizing that the discriminating variables were likely to be correlated with each other, we performed a principal components analysis (PCA) to reveal clusters of correlated variables. From the clusters, we selected representative variables that consistently exhibited strong bimodality across years, and that most closely matched the hypothesised basis for the ecotype distinction (Bergerud, 1988) on the proximal-distal spectrum (Austin, 2002; Dormann et al., 2007).

Visual inspection of the distributions of the discriminating variables revealed varying degrees of bi-modality. We estimated the strength of bimodality using a univariate adaptation of piecewise regression (e.g. Avgar et al., 2013), also known as broken-stick or changepoint regression. We hypothesised two, rather than n, ecotypes, so we iteratively applied a breakpoint increasing over the data range to successively partition the observations into two groups. At each step we computed an adjusted coefficient of determination (R²) from one-way, two-level analysis of variance of the discriminating variable, estimated using the Im procedure in R. We selected the breakpoint yielding the highest R^2 value. To avoid pseudo-replication, stemming from multiple observations of the same animal in different years, and because we were also interested in inter-annual variability, we estimated breakpoints and R^2 values for each year for each variable. We used these breakpoints to infer and assign an ecotype to each animal in each year. We compared the assignment consistency among the selected top discriminating variables, and also computed the consistency of assignment across years for animals with multiple years of observation.

Due to logistical constraints in the field, caribou collaring locations were widely separated (Fig. 1). To assess the potentially confounding effect of dispersed capture locations on an underlying monotonic response to a geographic gradient, we chose a subset of collaring localities where caribou of both ecotypes, by our classification, were collared. We examined the strength of discrimination for this subset of animals. We interpreted bimodality in this subset as support for discreteness of ecotype behaviours, not simply as a consequence of geographically separated capture locations. This analysis is described and reported in Appendix A.

2.3.2. Ecotype characteristics

Given classification of our collared animals into inferred ecotypes, we assessed the significance and effect size for other characteristics considered to vary by ecotype: chest girth and hind foot length; aggregation behaviour, calving date and seasonal range separation. For each variable, except range separation, we tested differences of means within each year, which avoided issues of pseudo-replication and also revealed the degree of inter-annual variability. We applied Welch's unequal variances t-test and report p values; in addition we report adjusted R² values to indicate ranking in cases where the p-values were <0.001.

To map ecotype ranges, we computed annual ranges in two ways using all locations of animals of each ecotype: (i) 100% minimum convex polygon (MCP) and (ii) 99% isopleth of a kernel density estimation (KDE) probability surface. MCP boundaries are sensitive to outliers, since the bounding polygon encompasses all points in a set. However, this potential for over-estimation is balanced to some degree by sampling, since our sample was unlikely to include caribou with the greatest range extents. KDE, on the other hand, produces an interpolated density surface based on local densities of animal locations. While allowing every point to contribute to the estimation of the boundary, KDE overcomes the strong outlier effect on estimated range extent characteristics of MCP. KDE likely produced a conservative estimate of range extent. We used both methods to assess annual ecotype range extents, degree of overlap and thus the confidence to place in these boundaries. To compare seasonal disjunction of ranges, we computed the area of intersection between the seasonal and annual MCP ranges for each ecotype, also expressed as the percentage overlap of seasonal and annual ecotype ranges.

3. Results

3.1. Ecotype discrimination

As anticipated, PCA indicated highly collinear data, with the first component accounting for 70% of the variance in the 9 variables, and the second accounting for an additional 12%. The bi-plot of the loadings (Fig. 2) clearly showed the collinearity, as well as bimodality of the data points on the first component. As a consequence of this collinearity, and because we were interested in the relative utility of individual variables for discrimination, we proceeded with univariate cluster analysis of each of the candidate discriminator variables independently. The second component can be characterized as a home range shape dimension; however, it does not offer additional discrimination power.

The results of the breakpoint cluster analysis (Table 2) showed that location variables were superior discriminators to movement and home range variables. The explanatory power for the movement and home range variables, averaged over the study period, did not exceed 80% and only one value in one year (MCP Area in 2012) exceeded 85% (Table 2). In contrast, location variables accounted for over 88% of the

BC 1 (Variance: 70.5%)

Fig. 2. Variable loadings and component scores for the first two components of the PCA of woodland caribou ecotype discriminating variables in northern Ontario. Dots represent animal-year observations; vectors represent (a) Ln(distance to treeline), (b) Ln(MCP Edge-to-area), (c) Ln(MCP Shape), (d) Ln(MCP Perimeter), (e) Ln(MCP Area), (f) Ln(Path length), (g) Percent locations in HBL, (h) Percent locations in CstHBL and (i) Percent locations in HB-IBL

Analysis of variance coefficients of determination (adjusted R²) for calving season variables used to assign female woodland caribou to ecotype groups; n is sample size.

		Calving season				
Variable type	Variable	2009 n = 85	2010 n = 104	2011 $n = 86$	2012 n = 27	Overall $n = 302$
Movement, home range	Ln(Path length)	0.712	0.791	0.773	0.829	0.736
size and shape	Ln(MCP Area)	0.711	0.784	0.791	0.861	0.751
	Ln(MCP Perimeter)	0.731	0.769	0.766	0.849	0.751
	Ln(MCP Edge-to-area)	0.695	0.796	0.789	0.842	0.744
	Ln(MCP Shape)	0.645	0.646	0.718	0.724	0.608
Location	Percent locations in CstHBL	0.884	0.905	0.950	0.777	0.880
	Percent locations in HBL	0.990	1.000	0.988	1.000	0.994
	Percent locations in HB-JBL	0.987	0.993	0.996	1.000	0.993
	Ln(distance to treeline)	0.863	0.889	0.869	0.965	0.872

total variation, with only one value less than 87%. In light of these results and our central hypothesis (Bergerud, 1988), we focused on Distance to Treeline for further analyses, complemented by the variable with the highest discriminatory power, Percent Calving Locations in the HBL (average $R^2 = 0.995$).

The assignment of each animal-year observation to ecotype by Distance to Treeline and Percent Calving Locations in the HBL was strong (Fig. 3) and consistent, with disagreement between the two assignment variables on only 3 of 302 animal-year observations. For classification by Percent Calving Locations in the HBL, none of the 101 animals with more than one year of data changed behaviours among years. Using Distance to Treeline as the discriminating variable, two animals with more than one year of data appeared to change behaviours over the study period. Examination of the subset of caribou collared in localities where both ecotypes were identified showed clear bimodality in both discriminating variables (Appendix A). Because of the high explanatory power (R^2) of Percent of Calving Locations, and the consistency of classification due to collinearity we used classification by Percent of Calving Locations in the HBL as the discriminator for ecotype in subsequent analyses.

3.2. Ecotype characteristics

In examining other putative ecotype characteristics, we found that neither of the two morphological measures differed significantly between ecotypes (Table 3). However, mean distances to nearest neighbour, indicative of herding behaviour, were significantly different in 2 of 4 years. The sedentary ecotype, as expected, spaced further from nearest neighbours than the migratory ecotype by an average of



Fig. 3. Frequency distributions of ecotype discriminating variables for female woodland caribou, 2009–2012, exhibiting strongest bi-modality.

Table 3

Results of Welch's difference of means test for morphological measures, nearest neighbour measures of aggregation and calving date for female woodland caribou in northern Ontario. Nearest neighbour tests were conducted on natural log-transformed data; reported means were from untransformed data. (n/a indicates testing was not appropriate because of lack of independence of observations).

		Sedentary ecotype mean	Migratory ecotype mean	Difference	Degrees of freedom	p-value	Adjusted R ²
Morpho-logical measures (cm)	Girth	118.5	116.8	-1.7	89.3	0.076	0.009
	Hind foot length	60.2	59.6	-0.7	118.9	0.091	0.004
Mean nearest neighbour	2009	39.6	44.8	-5.2	78.9	0.913	0.004
distance at calving (km)	2010	41.9	27.6	14.3	54.2	< 0.001	0.137
	2011	51.1	36.5	14.6	67.2	< 0.001	0.120
	2012	54.6	28.3	26.3	14.0	0.024	0.155
	Study period	44.5	34.0	10.5	n/a	n/a	n/a
Calving day of year (date)	2009	140.2 (20 May)	144.6 (24 May)	4.4	41.467	0.006	0.058
	2010	135.0 (14 May)	141.8 (21 May)	6.8	65.669	< 0.001	0.178
	2011	135.3 (15 May)	141.4 (21 May)	6.2	81.954	< 0.001	0.206
	Study period	136.6 (16 May)	142.3 (24 May)	5.7	n/a	n/a	n/a

14 km or more. Mean calving dates for migratory caribou were significantly later for migratory than for sedentary caribou by an average of 6 days across all years. However, in 2009, when mean calving date for sedentary caribou occurred approximately 4.5 days later than the other 2 years, the difference in calving dates between ecotypes dropped to 4.4 days (Table 3).

Maps of annual ranges, as defined by this sample of caribou, one based on the 100% MCP, portraying the maximum extent of range, the other based on the 99% KDE polygon — revealed partial disjunction between ecotypes in higher use areas (Fig. 4).

The geographic extent of the ecotype ranges indicated by annual MCPs showed a large overlap. Maps of seasonal ranges demonstrate a decline in overlap from early winter to calving as expected (Table 4, Fig. 5). This decline continued monotonically through the summer to a minimum of 2% of range overlap during the breeding season.

4. Discussion

Our study illustrates the use of animal movement and location data for intra-subspecies classification, as well as its utility for identifying units for conservation (Green, 2005; Mee et al., 2015) and understanding animal ecology (Morrison, 2012). Identification and ecological knowledge are precursors to risk assessment and the development of conservation plans. For *Rangifer*, the ecotype as a DU continues to be contentious in Ontario (Ontario Forest Industries Association, 2015; Schaefer and Ray, 2015). Our findings support the validity of the ecotype as DU for woodland caribou on the criteria of both discreteness and significance (COSEWIC, Committee on the Status of Wildlife in Canada, 2010). These ecotypes differ not only in their spatial behaviours (Figs. 4 and 5, Table 2; Avgar et al., 2013; Bergman et al., 2000), but also markedly in demography and population limiting factors (Bergerud et al., 2008; Festa-Bianchet et al., 2011).

Strong, discrete bi-modalities in the spatial behaviour of female caribou (Figs. 3 and 5, Tables 2 and 4) support the notion that these ecotypic differences stem from strategies to reduce predation on calves (Bergerud, 1988, 1996). The distinction – whether or not females give birth in the midst of predators and alternate prey – leads females to "space out" from each other (the sedentary ecotype) or to "space away" north of treeline into areas of lower predator density (Heard and Williams, 1992). Classification based on the strongest discriminator, Percent Calving in HBL, accounted on average for 99.5% of its variation, a result uninfluenced by the distribution of capture locations. Distance to Treeline also showed marked discriminatory power, with ecotype accounting for 87.2% of its variation (Table 2). As hypothesised, our findings revealed two discrete spatial behaviours in female caribou in Ontario, especially related to calving, and that these behaviours do not vary on a smooth gradient or continuum. Moreover, our study suggests the ecotype of an individual female may be permanent (see also Boulet et al., 2007). That there is no clear genetic distinction of the two ecotypes in this study area (COSEWIC (Committee on the Status of Wildlife in Canada), 2011; McQuade-Smith, 2009), suggests that the persistence of these spatial calving behaviours results from a "tradition" maintained by long-term spatial memory, which has been demonstrated in these caribou by Avgar et al. (2015). The consistency of behaviours over time is further evidence for the significance and uniqueness of these ecotypes as DUs.

As implied by the labels, sedentary and migratory, the extent of movements also might distinguish the ecotypes of *Rangifer* (Bergerud, 1988). In our study, discrimination based on space use (e.g. path length, home range size and shape) was also strong, with explained variance ranging from 64.5% to 86.1% (Table 2). Annual path length is analogous to mean monthly displacements (Avgar et al., 2013). While these authors reported a latitudinal breakpoint in movement rates attributable to ecotype differences, the distributions of their movement data were not clearly bi-modal. Our study extends the application of movement analysis to the detection of ecotypes and provides a means of assigning ecotype to individuals.

Rangifer exhibits geographic variation in body size (Geist, 1987), suggesting that morphology might also have discriminatory value. In our study, we assessed ecotype differences in morphology, aggregation behaviour and the timing of calving. Although some of these variables demonstrated significantly differing means, none had sufficient ecotype-related variability to be a reliable discriminator of individuals (Table 3). Morphological measurements, which might be useful for field identification and discrimination of ecotype, did not differ. Indeed, body size of large herbivores may be prone to temporal effects (Morellet et al., 2007). In Quebec-Labrador, for instance, the migratory George River caribou herd showed dramatic declines in stature in the late 20th century, likely owing to density-dependent food limitation. Over a few decades, they shifted from being larger than sedentary Mealy Mountain caribou to being smaller (Couturier et al., 2010).

"Spacing out" and "spacing away" (Bergerud et al., 2008) neatly encapsulate the strategies of female caribou to avoid predation. Although a crude measure of aggregation, the mean nearest neighbour distances among collared caribou in our study showed significant differences between ecotypes; the "selfish herding" characteristics of migratory caribou were evident (Table 3). Forming groups in the midst of wolves, swamps the predator for a short time (Fryxell and Sinclair, 1988; Skogland, 1991), and the predator, tied to its altricial young, is unable to move with the caribou as a continuing source of prey (Bergerud et al., 2008). Wolves in the Hudson Plain occur at lower densities than in the boreal forest (Berglund et al., 2014; Patterson, 2009; Poley et al., 2014). This implies that, in Ontario, the ecotone for distinguishing migratory caribou by calving location may not lie between the taiga and tundra, as proposed by Bergerud (1988), but rather between the forested upland of the Boreal Shield and the low-productivity lowlands of the Hudson Plain (Fig. 4).





Fig. 4. Annual ecotype ranges (a) 100% minimum convex polygon (MCP) delineation of caribou ecotype ranges with all caribou locations and (b) 99% kernel density estimation of caribou ecotype ranges.

Table 4

Seasonal MCP areas of intersection and percentage overlap for each ecotype of northern Ontario female woodland caribou.

Season (date range)	Area of intersection (km ²)	Intersection as percent of sedentary MCP	Intersection as percent of migratory MCP
Annual	170,517	43%	55%
Early Winter (1 Jan.–9 Feb)	120,836	37%	59%
Late Winter (10 Feb21 Mar)	99,897	33%	53%
Calving (1 May–9 June)	30,174	11%	19%
Summer (23 July-31 Aug)	5639	2%	3%
Breeding (9 Sep.–19 Oct)	4515	2%	2%

Drawing lines between ecotype characteristics has a geographic corollary. There was clear overlap in the composite ranges of the two ecotypes over the whole study period, particularly in winter, and the ecotypes may often intermingle during winter (Poley et al., 2014; Schaefer et al., 1999). In contrast, geographic separation during the rest of the year is remarkable, particularly during the breeding and calving seasons (Fig. 5). Separation at breeding time may be instrumental in maintaining maternally inherited genetic structure and could conceivably give rise to measurable genetic separation over the long term. Nevertheless, the ecotypic divisions of *Rangifer* (Bergerud, 1988) focus on females. Males are likely influential. Using microsatellite markers in Quebec-Labrador, Boulet et al. (2007) inferred that even low rates of incursion by migratory individuals, especially males, into sedentary ranges at breeding time could result in weak genetic population structure.

The implications of drawing lines are laid bare in Ontario. Here, the two ecotypes as DUs receive differing levels of protection under legislation: the Boreal Population (sedentary, forest-dwelling caribou) is listed as threatened; and the Eastern Migratory (forest-tundra) caribou is not listed (COSEWIC (Committee on the Status of Wildlife in Canada), 2002; OMNR, 2015). Therefore, mapping their ranges and understanding the temporal patterns of occupancy are important elements in conservation. We found consistent overlap between ecotype ranges encompassing the Hudson Plain — Boreal Shield ecotone (Fig. 5). Analogous to Quebec-Labrador (Boulet et al., 2007), there was a greater extension of migratory caribou into the Boreal Shield than sedentary animals onto the Hudson Bay Lowland. The overlap is seasonal; migratory caribou were generally in the Boreal Shield only during the winter. Our mapping results are reiterated two-fold: in the high probabilities of



Fig. 5. Seasonal ecotype MCP ranges for northern Ontario female woodland caribou.

winter occupancy by caribou along this ecotone (Poley et al., 2014) and in the breakpoint in the caribou movement rates at approximately 53.8°N, bisecting the southern boundary of Hudson Bay Lowland (Avgar et al., 2013).

With recognition that species-level classification may be too coarse for biodiversity conservation (Ceballos and Ehrlich, 2002; Clark et al., 2011; Morrison, 2012), the ecotype concept becomes useful in protection and conservation. Indeed, the concept has been instrumental to our understanding of Rangifer (Bergerud, 1996; Bergerud et al., 2008). However, ecotype can be analogous to the concept of cryptic species for conservation biology (Bickford et al., 2007). As our study underscores, consistent and discrete spatial behaviours are detectable only by detailed observation over time. It is clear that analysis of space-use by a species can reveal unique and significant sub-species groups not obvious by other means of assessment. Mapping ranges through these analyses meets a critical need for accurate population assessment. Range delineation is important when the groups are not readily distinguishable and their ranges overlap (Musiani et al., 2007; Oudejans et al., 2015; Torres et al., 2003). Knowledge of ranges will improve survey designs for population assessment, particularly in identifying areas where overestimation is a likely consequence of range overlap, but also in identifying optimal times to survey to minimize effects of cryptic groups. Finally, in the case of ecotypes which cannot readily be protected by regulations requiring field identification, conservation measures must be applied to geographic ranges and, if ranges overlap seasonally, then also at particular times in the year. Echoing Morrison (2012), we believe that the ecotype may represent the key unit to understand the ecology and life history requirements in support of species conservation.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at http://dx. doi.org/10.1016/j.biocon.2015.12.005.

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