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Delineating demographic units of woodland caribou (*Rangifer tarandus caribou*) in Ontario: cautions and insights

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Abstract: Delineating demographic structure across an organism's range can reveal the extent to which population dynamics in different geographic areas are driven by local or external factors and can be crucial for effective conservation and management. Obtaining optimal data for such analyses can be time and resource-intensive and impending development and resource extraction pressures may necessitate the examination of existing data, even when they are less than ideal. We analyzed a historic telemetry dataset containing satellite radio-collar locations of 73 forest-dwelling woodland caribou in northern Ontario to determine demographic structure. We applied several clustering methods (i.e., agglomerative, divisive and fuzzy *k*-means) to median seasonal locations. Results were used to distinguish demographic units and minimum convex polygons and fixed-kernel density estimates were used to delineate unit boundaries and core areas. For areas where sampling was considered representative of the distribution of caribou on the landscape, we assessed demographic distinctness by evaluating intra-individual variation in cluster membership, membership strength and distance between boundaries and core areas of adjacent units. The number and composition of clusters identified was similar among methods and caribou were grouped into 6 general clusters. The distinctions between the three clusters identified in the central portion of the province (i.e., Lac Seul, Wabakimi, Geraldton) and the two clusters identified in the eastern portion of the province (i.e., Cochrane and Cochrane-Quebec) were determined to represent demographic structuring. Additional distinctions in other areas (i.e., between The Red Lake and Lac Seul clusters in the west and between the central and eastern clusters) may just be artifacts of the original sampling effort. Amongst demographic units, there was no evidence of individual flexibility in cluster membership and average membership strength was very high. There was little to no overlap between boundaries and core areas of adjacent units, but distances between adjacent unit boundaries were relatively low. Additional sampling effort is needed to further delineate demographic structure in Ontario caribou.

Key words: cluster analysis; demographic units; Ontario; population delineation; population monitoring; *Rangifer tarandus caribou*; woodland caribou

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Introduction

Determining population structure is a critical step for developing effective wildlife conservation and management strategies (Bethke *et al.*, 1996; Thomas & Kunin, 1999; Schaefer & Wilson, 2002; Edwards *et al.*, 2008; EC, 2008). If discrete local populations exist, their boundaries can serve as an ecologically meaningful basis for determining abundance and rates of population change (Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; EC, 2008) — information that is essential for standard assessments of population viability (Akçakaya & Sjögren-Gulve, 2000). If data on survival, pregnancy and recruitment are summarized over areas that fail to correspond with the spatial distribution of demographically distinct groups of individuals, then the resulting estimates of vital rates may be inaccurate and unreliable for conservation and management purposes (Bethke *et al.*, 1996; Edwards *et al.*, 2008). Unreliable estimates of population sizes and trends could have serious consequences for long-term population viability, particularly for organisms whose long-term persistence is threatened.

The northern region of Ontario encompasses approximately 18% of the extant range of what the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) refers to as the "boreal population" (Thomas & Gray, 2002) of the forest-dwelling ecotype of woodland caribou (*Rangifer tarandus caribou*). The boreal population has exhibited long-term patterns of range retraction and population decline (Racey & Armstrong 2000; Schaefer, 2003) and these trends have resulted in a "threatened" species designation under Canada's federal *Species at Risk Act* (2004) and Ontario's *Endangered Species Act* (2007). Consequently, there have been several recent national and provincial efforts to develop conservation and recovery strategies for woodland caribou (e.g., MC, 2005; EC, 2008; OWCRT, 2008; OMNR, 2009).

The Scientific Review for the Identification of Critical Habitat for Woodland Caribou (*Rangifer tarandus caribou*), Boreal Population, in Canada (EC, 2008) recommended that each jurisdiction currently occupied by the boreal population of woodland caribou undertake efforts to delineate local populations and ranges and use these as units of analysis for assessing population trends and probability of persistence. Due to the difficulties associated with inferring demographic structure from genetic indicators (Avise, 1992; Cronin, 1993; Moritz, 1994; Esler *et al.*, 2006; Palsbøll *et al.,* 2007; Frantz *et al.,* 2009), the *Scientific Review* recommended that telemetry-based analyses of individual space use and movement patterns of forest-dwelling woodland caribou be used to delineate meaningful demographic units (i.e., "local populations") throughout the ecotype's current range (EC, 2008: Appendix 6.2).

The ideal dataset for such analyses would be obtained via a uniform distribution of sampling effort throughout the current range of forest-dwelling woodland caribou (e.g., Schaefer *et al.*, 2001; McLoughlin *et al.*, 2002). Sample sizes would be sufficiently large and study duration sufficiently long (e.g., 20 years - EC, 2008: Appendix 6.2) to capture spatial and temporal variability in movement behaviour and radiocollar deployments would be representative of the distribution of caribou across the landscape (e.g., uniform, patchy). For wide-ranging, long-lived species like woodland caribou, obtaining such an optimal dataset would require extensive resources and considerable time. In situations where resource extraction and development pressures are high, it will sometimes be necessary to evaluate existing data and if adequate, analyze them to derive preliminary assessments of demographic structure, which can be used to make conservation and management decisions that cannot be deferred until more comprehensive datasets are available. While such analyses should not be used as a substitute for initiating more comprehensive studies, they can be used to inform management decisions until more appropriate sources of information are available.

In Ontario, there have been several research and local management-based projects over the past 15 years that have deployed satellite radiocollars on forest-dwelling woodland caribou. For much of this time period, collars were only deployed near the southern margin of the ecotype's continuous range within the province and even within this general area, sampling efforts were not evenly distributed and the temporal extent of data coverage differs substantially between regions. While these data are not ideal for delineating population structure, industrial pressures within the continuous range are high and will likely increase as development (e.g., roads, utility lines) and resource extraction activities (e.g., mining and forestry) expand northwards (OMNR, 2008). Thus, there is justification for evaluating existing telemetry data for Ontario's woodland caribou as a means of obtaining preliminary insights into demographic structure in the portion of their range where they are considered at greatest risk of extirpation (Racey & Armstrong, 2000; Thomas & Gray, 2002; Schaefer, 2003).

In this study, we applied the same general methodology used in several other studies of species' demographic structure (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; McLoughlin *et al.*, 2002; Edwards *et al.*, 2008) to delineate preliminary demographic units of forest-dwelling woodland caribou at the southern limits of their continuous range in Ontario.

First, we inspected the distribution of deployment locations to determine which regions of the province had data that were adequate for delineating demographic units. Second, we applied several different cluster analysis techniques to satellite telemetry data to determine whether there is evidence for spatial population structure amongst these woodland caribou. Third, we used home range estimators to delineate the boundaries and core areas of use associated with identified groups. Fourth, we looked at evidence for immigration/emigration and the proximity of boundaries and core areas amongst adjacent groups to determine whether they are demographically distinct. Finally, we discuss the implications of the results for identifying areas where additional research and monitoring are needed to develop effective conservation and management strategies for forest-dwelling woodland caribou in Ontario.

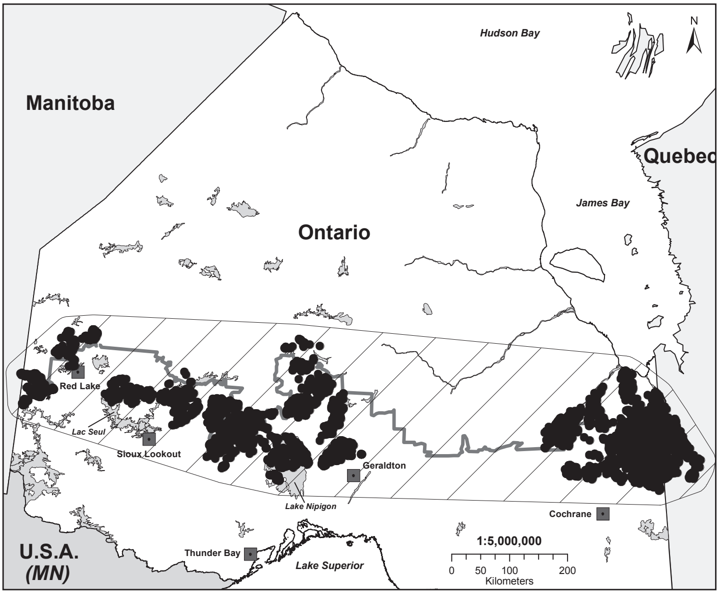

Fig. 1. Study area and locations of sampled individuals. Hatched polygon delineates the general study area, defined by a buffered (25 km) 100% Minimum Convex Polygon. Black circles represent all sub-sampled locations recorded from 1995-2008, for the 73 woodland caribou (*Rangifer tarandus caribou*) included in our analyses. Thick gray line depicts the northern boundary of commercial logging during the time period when location data were collected.

Material & methods

Study area

The study area (Fig. 1) was located in northern Ontario, Canada. It was approximately 236 000 km^2 in size, spanning a 1185 km distance from east to west (78°36'W to 95°13'W longitude), and a 255 km distance from north to south (51°48'N to 49°36'N latitude). It encompassed eastern and western sampling regions, which were separated by an area (spanning approximately 320 km from east to west) where no sampling was conducted.

The western sampling region fell within Canada's boreal shield ecozone (Wiken *et al.*, 1993) and was located almost entirely within the region subjected to commercial logging. It is described in detail by Ferguson & Elkie (2004a, 2004b, 2005). Forest cover was dominated by jack pine (*Pinus banksiana*) and also contained black spruce (*Picea mariana*), balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), white birch (*Betula papyrifera*) and trembling aspen (*Populus tremuloides*) (Rowe, 1972). The topography has been characterized as rolling and relatively low relief, featuring well-drained soils, sand and gravel deposits and rocky uplands and outcrops (Rowe, 1972). The landscape contained numerous bogs, fens, rivers and lakes, including a few larger waterbodies such as Lake Nipigon and Lac Seul (Rowe, 1972). The primary source of natural disturbance was wildfire, with return intervals ranging from 80 to 200 years (Li *et al.*, 1996 cited in Ferguson & Elkie, 2004a).

The eastern sampling region straddled the boundary between Canada's boreal shield ecozone in the south and the Hudson Plains ecozone to the north (Wiken *et al.*, 1993). It was located in the "clay belt" region of north-eastern Ontario (Rowe, 1972) and is described in detail by Brown *et al.* (2003, 2006, 2007). Forests in the southern half of the region fell within the area of the province where commercial logging was permitted, while forests in the northern half were not subject to this disturbance type. The topography in this sampling region is relatively flat, soils are dominated by water-worked tills and lacustrine materials and forest cover is dominated by lowland black spruce stands, interspersed with numerous treed bogs, sedge fens and sphagnum-heath bogs, but relatively few lakes (Rowe, 1972; Brown *et al.*, 2007). Species such as tamarack (*Larix laricina*), trembling aspen, willow (*Salix* spp.), balsam fir and white birch co-occur with black spruce in early successional stands, while mixedwood or jack pine-dominated stands sometimes occurred in drier sites (Rowe, 1972; Brown *et al.*, 2007). The primary sources of natural disturbance were wildfire and insect infestation (Carleton & Maycock, 1978), with fire return intervals estimated at approximately 263 years (Ter-Mikaelian *et al.*, 2009).

Animal capture and telemetry

Capture and handling procedures

In the western sampling region, a total of 53 forest-dwelling woodland caribou (40 adult females, 13 adult males) were captured and collared by Ontario Ministry of Natural Resources (OMNR) staff from 1995 to 2005. Animals were captured using net-guns during winter (*n*=31) or while swimming during spring and summer (*n*=22). Fifty caribou were fitted with an Argos radiocollar that contained both satellite (UHF) and VHF transmitters (Telonics, Inc., Mesa, AZ, U.S.A.) and three caribou were fitted with

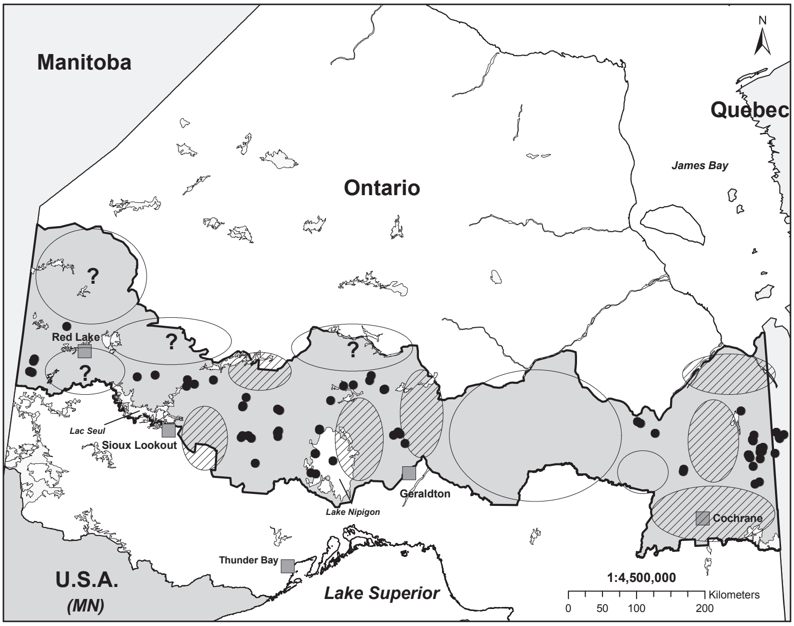

Fig. 2. Approximate deployment locations (black circles) of radio collars placed on forest-dwelling woodland caribou in Ontario from 1995 to 2008. Only deployment locations of individuals included in the cluster analysis (*n* = 73) are depicted. The gray polygon is bounded by the southern boundary of the ecotype's continuous distribution in the province (OMNR 2009) and the approxmate northern extent of historic sampling efforts in the province. The hatched ellipses represent areas where spatial gaps in deployment locations correspond with apparent low density areas for caribou (assessed during winter). Hollow ellipses without question marks represent areas where spatial gaps in deployment locations are known to be artefacts of inadequate sampling efforts. Hollow ellipses with question marks represent areas where further sampling efforts are needed to determine whether spatial gaps in deployment locations reflect low caribou density or whether they are artefacts of inadequate sampling effort.

GPS "store on board" radiocollars (Lotek Wireless Inc., Newmarket, ON, Canada).

In the eastern sampling region, a total of 36 female caribou (32 adults and 4 yearlings) were captured and collared by OMNR staff. Thirty collars were deployed in the Detour Lake area in 1998 and 1999 (Brown *et al.,* 2003) and in 2006, six additional collars were deployed just west of the region sampled during the first period (Gauthier, 2007). All animals (*n*=36) were captured during winter and were herded into nets using a helicopter and ground crew (Brown *et al.*, 2003; Gauthier, 2007). Once captured, each caribou was fitted with an Argos radiocollar that contained both satellite (UHF) and VHF transmitters (Telonics, Inc., Mesa, AZ, U.S.A.) Capture and handling procedures for all 89 collared caribou followed several similar protocols, all of which were approved by the OMNR Animal Care Committee.

Sampling efforts

As mentioned above, sampling efforts were not evenly distributed throughout the study area. In some cases, efforts were made to distribute radiocollars in a manner that represented the distribution of caribou on the landscape, while in others, sampling was concentrated in areas of local management concern or sample sizes were simply too small to obtain adequate regional coverage. The approximate deployment locations of radiocollars on caribou included in our analyses (see "Cluster Analysis" below) are depicted in Fig. 2.

In the central-west and the eastern-most sections of the study area the distribution of deployment locations was relatively even (Fig. 2). Additionally, based on the average annual home range sizes for woodland caribou in the boreal shield ecozone in northwestern Ontario (i.e., 1148 km^2 ± 109 km^2 SE – derived from generating 100% MCPs using the annual telemetry data of each individual analyzed here) and the boreal clay plains ecozone in northeastern Ontario (i.e., 4026 km^2 ± 29 km^2 – Brown *et al.,* 2003), we determined that sampling resolution in most areas was sufficient to allow for potential home range overlap between adjacent collared animals. Despite these generalities, there are some areas in these regions where there were spatial gaps in the distribution of deployment locations—immediately east of Lake Nipigon and immediately northeast of Geraldton, east and north east of Sioux Lookout and Lac Seul, as well as the northern and central portions of the area north of Cochrane (Fig.e 2: hatched polygons). However, recent efforts to distribute radiocollars as uniformly as possible in each of these general areas confirmed the absence of caribou or, at best, occurrence at extremely low densities (A. Rodgers, OMNR, unpubl. data, 1 April 2011; L. Walton, OMNR, pers. comm., 25 March 2011). This indicates that the patchiness of historic collar deployments in the specific areas described above is likely representative of the distribution of individuals across the landscape during sampling and not due to lack of effort.

In contrast, there were other areas where inadequate sample sizes and/or spatial contagion in sampling effort made it impossible to infer demographic structure from the available telemetry data (Fig. 2). Specifically, there was a total absence of historic sampling effort in a large area between the eastern region and the central region of the study area (Fig. 2: hollow polygons, no question marks) and recent sampling efforts in this area resulted in several collar deployments (L. Walton, OMNR, pers. comm., 25 March 2011), indicating that caribou are currently present and likely had a historic presence in this area.

Small sample sizes and spatially clustered deployments in the western-most section of the study area (i.e., the area to the north and west of Lac Seul and the Red Lake area – Fig. 2: hollow polygons with question marks) also made it difficult to draw demographic inferences using the telemetry data collected in this region. Consequently, fine scale analyses of core areas and proximity (see below) were not undertaken for either of these areas. Additional collaring efforts are needed in this latter group of areas to determine whether the spatial gaps in deployment locations highlighted in Figure 2 represent areas of low caribou use or whether they are artefacts of inadequate sampling efforts.

Observations made during recent collaring efforts (L. Walton, OMNR, pers.comm., 25 March 2011) indicate that the historic collar deployment locations north of Cochrane are generally representative of the winter distribution of caribou in this region (Fig. 2). However, the sample size in the western portion of this general area was considered to be too small to complete fine scale analyses of core areas and proximity using historic data. Thus, only coarse delineations of range boundaries and assessments of boundary proximity were conducted in this area.

Radiocollar transmission schedules

Collars were scheduled to transmit or store caribou locations at time intervals that varied greatly among individuals (i.e., daily to every 10 days) and for 65 of the caribou with Argos satellite collars, between seasons (i.e., every two days for spring and autumn, every 7 days for late winter and summer). For both the Argos satellite and GPS collars, multiple locations were often estimated during each day in which data transmission or storage occurred. A total of 60 403 locations were obtained from the original 89 collared individuals.

Cluster analyses

Data preparation

Since the analysis focused on identifying demographic structure amongst woodland caribou in Ontario, we excluded any individuals with collaring periods that were too short to provide representative location information throughout the course of the annual cycle (e.g., McLoughlin *et al.*, 2002). The length of the collaring period for each individual was calculated and only those individuals with collaring periods ≥ 0.75 years (n = 73) were included in subsequent analyses. Of the 73 individuals (64 females, 9 males) that remained, 34 individuals were collared for two full years and seven were collared for three full years, yielding a total of 121 individual-years of location data.

Next, the locations for the remaining individuals were screened for accuracy and all locations with relatively high error estimates were excluded from further analyses. For the Argos satellite data, only locations with Argos location quality index values of 3 (NQ < 250 m) or 2 (250 m ≤ NQ < 500 m) (CLS, 2008) were retained, while for the GPS data, only those locations with error estimates < 50 m were kept. Error estimates for GPS locations were based on position dilution of precision (PDOP) values and the number of dimensions associated with each position (i.e., 2D or 3D). Finally, in circumstances where individuals had multiple locations per transmission/storage period that met accuracy requirements, only the location with the highest accuracy was retained. If multiple locations met this criterion, the location associated with the earliest time of day was selected.

Both Argos satellite and GPS collars recorded location information using decimal latitude-longitude coordinates. To prepare the data for use in subsequent analyses, each location was “flattened” or scaled to a common x,y grid (Bethke *et al.*, 1996; Taylor *et al.*, 2001). A Lambert Conformal Conic (LCC) projection was chosen because it retains the relative Euclidean distance between points (Taylor *et al.*, 2001). ArcGIS (v. 9.2, ESRI, Inc.) was used to reproject the geographic dataset in the LCC format.

Seasonal median locations

Forest-dwelling woodland caribou in Ontario exhibit seasonal changes in movement behaviour and habitat selection (Cumming & Beange, 1987; Bergerud *et al.*, 1990; Brown *et al.*, 2003; Ferguson & Elkie, 2004a). To account for the seasonal shifts in spatial location that this might produce, we used the behavioural season definitions derived by Ferguson and Elkie (2004a) for woodland caribou in northwestern Ontario, to divide the location data into different seasons. Ferguson and Elkie (2004a) made a distinction between five different seasons based on temporal changes in movement rates: early winter, late winter, spring, calving and post-calving. However, because we wanted to minimize the ratio between observations and variables included in the cluster analysis and because spatial displacement and differences in movement rates between the calving and post-calving seasons were relatively low (Ferguson & Elkie, 2004a), we decided to lump these two seasons together. This produced a total of four different seasons: early winter (Nov. 15 – Jan. 20), late winter (Jan. 21 – Mar. 5), spring (Mar. 6 – May 5) and snow-free (May 6 – Nov. 14).

The start and end dates of these behavioural seasons did not correspond with the start and end dates used to set the seasonal transmission schedules that were applied to most of the deployed Argos collars. Therefore, for the 65 caribou with seasonally variable location intervals, location data were sub-sampled within seasons to ensure equal time intervals between sequential locations. After sub-sampling, median easting and northing values were estimated for each season, for each individual, for each year of location data, as recommended by Bethke *et al.* (1996), Taylor *et al.* (2001) and Schaefer *et al.* (2001). Thus, for every full year that an individual was collared, a total of eight variables (i.e., a median easting and northing value for each of four seasons) were derived to represent its general geographic location. For the 41 individuals that were collared for multiple years, calculating seasonal median locations separately for each complete year of data enabled each unique individual-year combination (i.e., "caribou-years") to be treated separately in the cluster analyses. Using caribou-year combinations as experimental units in the cluster analyses allowed us to detect migration between demographic units by allowing for the possibility of cross-classification of individuals to different clusters in different years (Taylor *et al.*, 2001; McLoughlin *et al.*, 2002).

Data analyses

To determine whether there was evidence for demographic structuring amongst forest-dwelling woodland caribou in Ontario, we performed cluster analyses on the seasonal median location data for each caribou-year. Clustering is a classification technique that forms groups of objects based on a measure of dissimilarity with respect to the independent variables included in the analysis (Romesburg, 1984; Kaufman & Rousseeuw, 1990). In this case, clusters of caribou-years were formed based on similarity in geographic location (i.e., their spatial proximity to one another).

Since the independent variables consisted of the geographic coordinates of an individual's position in space (east-west or north-south) during a particular season and year, Euclidean distance was selected as the measure of dissimilarity for the cluster analysis (Ferguson *et al.*, 1998; Schaefer *et al.*, 2001, Taylor *et al.*, 2001; McLoughlin *et al.*, 2002). Standardization of independent variable values to the zero mean is recommended in situations where independent variable values are measured in different units and/or the researcher wants to assign equal weight to variables with unequal variances (Romesburg, 1984; Gotelli & Ellison, 2004). Marked differences in the breadth of the study area along the east-west and north-south axes meant that variances in median easting values were substantially higher than variances in median northing values. However, since there was no *a priori* rationale for treating Euclidean distances between median locations along the north-south axis differently than Euclidean distance along the east-west axis and since all variables were measured using the same units of measurement, cluster analyses were performed using an unstandardized data matrix.

There are many different clustering methods that can be used to classify objects into groups. They differ in several respects, including (1) the basic type of clustering algorithm applied (e.g., partitioning, hierarchical), (2) the specific clustering procedure used (e.g., 'top-down' hierarchical divisive routines, 'bottom-up' hierarchical agglomerative routines), (3) the amalgamation or linkage rules for joining or separating hierarchical clusters and (4) whether cluster membership is absolute or partial (Anderberg, 1973; Romesburg, 1984; Kaufman & Rousseeuw, 1990). Some approaches are better suited to particular types of data than others (Romesburg, 1984), but applying multiple appropriate clustering methods and comparing results can serve as a test of whether the cluster structure identified is robust to methodological differences (Romesburg, 1984; Bethke *et al.*, 1996). With this in mind, we performed cluster analyses of the seasonal median location data using five different methods. These included the hierarchical divisive method, three hierarchical agglomerative methods (unweighted pair- group method with arithmetic mean [UPGMA], Ward's minimum variance method and the complete linkage method), and a partitioning clustering method (fuzzy *k*-means clustering). All hierarchical clustering methods were implemented in S-Plus v.6 (Insightful Corp., Seattle, WA, U.S.A.) and fuzzy *k*-means clustering was conducted using FuzME v.3.5b (Minasny & McBratney, 2002).

Fuzzy *k*-means analysis permits objects to have partial membership across multiple clusters (Bezdek *et al.*, 1984; Odeh *et al.*, 1992). To set the fuzziness of the resulting classification, a weighting exponent (*m*) must be specified (Bezdek *et al.*, 1984; Schaefer *et al.*, 2001). We ran the analysis with the weighting exponent set at $m = 1.5$ to produce a low-to-moderate level fuzzy classification. Repeating the analysis with different values of *m* (changed in increments of 0.1) for $1< m \leq 2$ (e.g., Schaefer *et al.*, 2001) produced results that were qualitatively consistent in terms of cluster number and cluster membership.

Hierarchical clustering methods continue lumping or splitting objects into clusters until no new groups are possible, while partitioning methods require *a priori* specification of the total number of clusters (*k*) to be defined (Romesburg, 1984). Both approaches are associated with different options for determining the appropriate number of clusters. For the hierarchical methods applied, we determined the number of meaningful clusters based on notable changes in linkage distance when new 'splits' (for the divisive method) or 'lumps' (for the agglomerative methods) were formed (Schaefer *et al.*, 2001). For the fuzzy *k*-means analysis, we ran the analysis for $k = 2$, up to $k = 15$ and inspected values of separate fuzzy validity (S), the fuzziness performance index (FPI) and modified partition entropy (MPE) to identify the appropriate number of clusters (Reyniers *et al.*, 2006).

Once the appropriate number of clusters was determined, the results for each clustering method were compared to assess the robustness of cluster structure to changes in methodology. Comparisons were based on the number of meaningful clusters identified and cluster membership (i.e., the specific caribou-years assigned to each cluster). In cases of discrepancy between results produced by different methods, we determined final cluster structure by examining all location data for each caribou-year assigned to the affected clusters and considered the relative reliability of different clustering methods. For the location data, we calculated the distance between caribou-years in different clusters and determined the direction and extent of individual movements at cluster boundaries. For the methodological assessment, we considered the findings of previously published simulation studies that compared the performance of different clustering methods.

Under optimal sampling conditions, a cluster analysis of data from an unstructured panmictic population (i.e., the null hypothesis) would yield no significant clusters. However, inadequate sampling in two regions of the study area (i.e., between the eastern and central regions and between the Lac Seul and Red Lake areas – Figure 2) were expected to produce significant clustering even if the underlying population structure was panmictic. Thus, using the dataset described here, the null hypothesis was predicted to produce a three cluster solution (i.e., dividing the study area into western, central and eastern clusters). Under the alternative "demographic structure" hypothesis, cluster analysis was predicted to result in the detection of ≥ 4 significant clusters.

Delineating demographic units: boundaries and "core areas"

Selection of range estimators

To delineate demographic unit boundaries and identify areas of more intensive use (i.e., "core areas") within them, we pooled the location data for each caribou-year assigned to a specific cluster and applied two different home range estimators to the data for each cluster—Minimum Convex Polygons (MCPs) and Kernel Density Estimators (KDEs). We calculated 100% MCPs for each cluster because they provide an estimate of the total area used by sampled demographic unit members (Powell, 2000). Consequently, all locations analyzed are included within the resulting boundary and as such, the MCP can be viewed as a conservative estimator of the range associated with a given demographic unit (EC, 2008: Appendix 6.2). In comparison, ranges delineated using a KDE approach are generally smaller and outlying locations are not necessarily encompassed by isopleth boundaries (Powell, 2000; EC, 2008: Appendix 6.2). However, the resulting utilization distributions are based on information contributed by all locations and provide an estimate of the probability of occurrence of sampled demographic unit members within a range (White & Garrott, 1990; Seaman & Powell, 1996). This enables the delineation of boundaries and core areas for each demographic unit based on areas of frequent use.

For some clusters, limited sampling efforts restricted the extent to which clusters could be considered representative of demographic units and home range estimates could be considered representative of demographic unit boundaries and core areas. While we still applied MCP and KDE estimators to the sub-sampled telemetry data for these clusters, we only present 100% MCPs and 95% isopleths for these clusters. These are interpreted as providing a very preliminary indication of the minimum spatial extent of forest-dwelling woodland caribou demographic groups in these areas.

Data preparation

Since there was considerable variation in sampling intensity between caribou-years, we attempted to standardize the location data so that each caribou-year contributed a comparable number of locations per season. To accomplish this, we followed a protocol similar to the one described by Edwards *et al.* (2008). First we calculated the mean number of locations per season for the 65 caribou that were sampled at the coarsest time intervals (i.e., every seven days during summer and every two days during autumn and spring). Then, for the seven caribou that were sampled more frequently, we chose a random subsample of locations per season, per year for each caribou that was equal to the mean number of locations that we calculated for each season using the coarsely sampled individuals.

For KDE-based delineations of demographic unit boundaries and core areas, there was some concern that the results of analyses that included location data from every caribou-year would be unduly influenced by the geographic affinities of the 41 individuals who were collared for multiple years. To avoid this potential source of bias, we randomly selected one caribou-year per individual for inclusion in each cluster-specific analysis and excluded the data from other caribou-years. Since MCPs are delineated based on information from outer-most locations only, the inclusion of data for multiple years for the same caribou in a cluster-specific analysis was not considered problematic. Consequently, all of the data recorded for each individual were retained for the MCP-based delineations of demographic unit boundaries.

Data analyses

We used Hawth's Tools (Beyer, 2004) in ArcGIS v. 9.2 (ESRI, Inc. Redlands, CA, U.S.A.) to generate a 100% MCP for each identified cluster, using the sub-sampled location data for each caribou-year assigned to a given cluster during the cluster analysis. Fixed-kernel density estimates (Wand & Jones, 1995; Seaman & Powell, 1996; Taylor *et al.*, 2001) of demographic unit boundaries and core areas were derived using the Home Range Tools extension v. 1.1 (Rodgers *et al.*, 2007) in ArcGIS v. 9.2. Utilization distributions were derived using all of the sub-sampled data for each cluster that met the constraints outlined above (i.e., one randomly selected year, per individual, per cluster). A cell size of 150 x 150m was used to calculate the probability density of caribou locations for each demographic unit and 95% and 50% isopleths derived from the density function were used to delineate range and core boundaries, respectively.

KDE-based utilization distributions can be sensitive to choice of smoothing parameter and there is no general agreement on the optimal smoothing technique (Silverman, 1986; Gitzen & Millspaugh, 2003; Millspaugh *et al.*, 2006; Edwards *et al.*, 2008). To avoid under-smoothing or over-smoothing the utilization distributions, we used an *ad hoc* approach (e.g., Berger & Gese, 2007; Edwards *et al.*, 2008) to select cluster-specific smoothing parameters. For each demographic unit the "reference" smoothing parameter (h_{ref}; Silverman, 1986) was calculated, the resulting value was used as a starting h value and then h was increased or decreased by computing different proportions of h_{ref} in sequential increments of 0.01 until the minimum value of h that still produced a continuous, lacuna-free 95% isopleth, was identified (Silverman, 1986; Berger & Gese, 2007; Edwards *et al.*, 2008). The h value ($h_{\mathrm{ad\ hoc;}}$ Berger & Gese, 2007) identified for a given demographic unit served as the smoothing parameter for the utilization distribution constructed for that unit.

Assessing distinctness of demographic units

Our objective was to determine whether there was evidence for the existence of discrete demographic units. We applied two basic criteria to assess whether demographic units identified and delineated using cluster analysis and home range estimates could be considered demographically distinct from one another. The first criterion focused on the strength and consistency of caribou-year classification in the cluster analyses. To assess the level of uncertainty in the cluster membership assignment for each caribou-year, we examined the fuzzy membership coefficient values generated by the fuzzy *k*-means analysis. Additionally, to determine whether there was any evidence of migration between clusters, we conducted within-individual evaluations of cluster membership assignments amongst individuals collared for multiple years to identify between-year differences in cluster membership (e.g., Taylor *et al.*, 2001).

The second basic criterion that we applied to assess the demographic "distinctness" of identified clusters focused on the degree of geographic separation between boundary and core areas delineated for adjacent groups of caribou (EC, 2008: Appendix 6.2). First, we used the equation developed by Lazo (1994) to calculate the proportion of overlap between the MCP and KDE-based boundaries of adjacent clusters. Next, for core areas and boundaries that didn't overlap, we measured the minimum distance between the respective core areas and boundaries of adjacent clusters.

Assessing reliability of demographic units

Environment Canada (2008: Appendix 6.2) suggested that when the relationship between number of observations and cluster size is plotted, the presence of an asymptote indicates that corresponding cluster boundaries have a high probability of accuracy. Given the general fidelity that woodland caribou tend to exhibit at the home range scale (Ouellet *et al.*, 1996; Schaefer *et al.*, 2000; Rettie & Messier, 2001; O'Brien *et al.*, 2006), incremental changes in the number of locations based on the addition of data collected for single individuals appeared to be the most appropriate approach for evaluating this association. To assess the extent to which identified clusters could be considered representative of existing demographic structure, we applied an adapted version of the protocol suggested by Environment Canada (2008: Appendix 6.2). For each cluster, we randomly selected a single individual and calculated the area of the 100% MCP generated using their location data. We added the locations for each additional individual assigned to the cluster (in random order) and calculated the area of the corresponding 100% MCPs each time a new, randomly selected individual was included. The process was repeated until the locations for all individuals assigned to a cluster were included in the home range area calculations. Then, for each cluster, we inspected the relationship between 100% MCP size and the number of individuals that contributed to the corresponding estimate to determine if sampling efforts were sufficient for obtaining an accurate depiction of the size and location of cluster boundaries and cores.

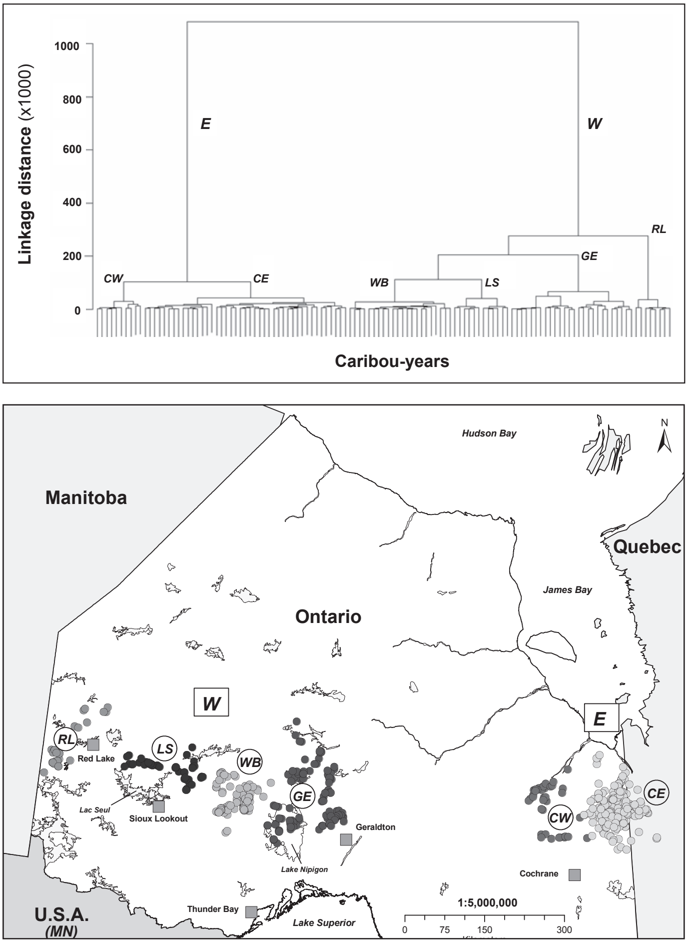

Fig. 3a-b. Cluster dendrogram formed from Euclidean distances between means of last clusters joined using the sum of squares (i.e., "Ward's") method (a) and geographic extent of corresponding clusters (b), depicted using the seasonal median locations of classified woodland caribou (n=73). Each terminal point in (a) represents one object (i.e, caribou-year), which include 1 full year of location data for a single individual. In both figures, the western and eastern sampling regions are labeled "W" and "E", respectively. The six clusters delineated were: Red Lake = "RL", Lac Seul = "LS", Wabakimi = "WB", Geraldton = "GE", Cochrane West = "CW", Cochrane East = "CE".

Results

Cluster analyses

General

Each of the different clustering methods yielded similar results with respect to cluster composition and the appropriate number of clusters. A dendrogram that depicts the results obtained when Ward's algorithm was applied to the seasonal median location data is depicted in Fig. 3a, to serve as an illustrative example of the groups demarcated by the different methods. Fig. 3b displays the geographic locations of the clusters detected using Ward's algorithm.

For all methods, the 3-cluster solution corresponded with the null hypothesis (i.e., panmictic population structure). The first split separated caribou in the east from caribou in the west and the second split separated caribou in the Red Lake area from other western groups (e.g., Fig. 3a), which corresponded with the cluster structure expected as an artifact of incomplete sampling efforts. Given the lack of sampling on the landscape between these clusters, it was impossible to determine the extent to

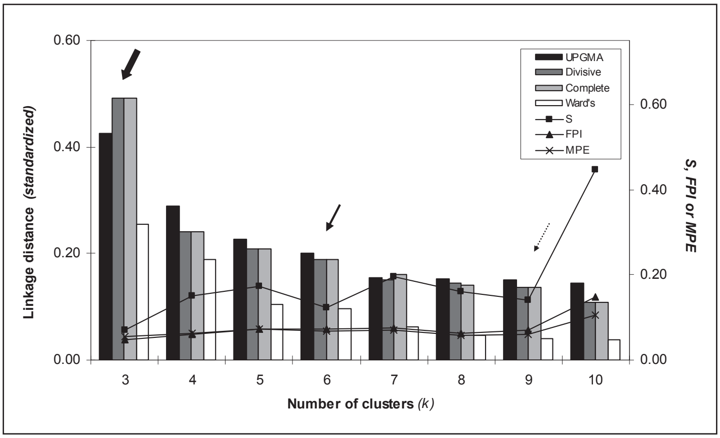

Fig. 4. Linkage distance (standardized across hierarchical methods) and fuzzy *k*-means performance measures in relation to number of clusters (*k*). Fuzzy performance measures include separate fuzzy validity (S), the fuzziness performance index (FPI) and modified partition entropy (MPE). The large solid arrow indicates the solution (k = 3) that corresponds with the null hypothesis (i.e., panmixia). For the hierarchical methods, the decline in linkage distance reached a plateau at k = 5 or 6 (indicated by the small solid arrow). Minimum values for the three fuzzy performance measures were observed at k = 3, with local minima at k = 6 and 9 (indicated by the small dashed arrow).

which these distinctions were representative of actual demographic structure. Consequently, we restricted our evaluation of the results and our demographic inferences to solutions with more than three clusters.

The relationship between the number of clusters and the different metrics used to identify the appropriate stopping point for different clustering solutions is depicted in Fig. 4. The minimum values for the 3 fuzzy indices corresponded to a 3 cluster solution (Fig. 4). For more complex solutions, FPI and MPE remained close to this minimum value until increasing at $k > 9$ (Fig. 4). In comparison, S was considerably higher than the minimum value for most of the more complex clustering solutions, increasing substantially when $k > 9$ (Fig. 4). Exceptions occurred at k = 6 and 9, where S reached local minima (Fig. 4).

For the hierarchical methods, the 3 cluster solution size was also associated with relatively high linkage distance, yet the decline in linkage distance continued as the number of clusters increased with all methods, indicating a general plateau in linkage height for solutions with more than 5-6 clusters (Fig. 4). Since all three fuzzy clustering indices were close to minimum values at 6 clusters and the S exhibited a local minimum when k = 6, clustering solutions that included 6 clusters appeared most appropriate for delineating demographic structure (Fig. 4).

The clusters delineated were relatively consistent across methods in terms of the location and composition of cluster solutions that contained 3 through to 6 clusters. Amongst the 6 cluster solutions, all methods delineated the same groups of caribou-years in the Red Lake area, Lac Seul area and the Cochrane area (which was subdivided into separate eastern and western groups) (Fig. 5).

The central area of the province was the only region where there were discrepancies among classifications produced by different methods. Specifically, cluster solutions differed in terms of how caribou-years with median locations in the immediate vicinity of Lake Nipigon were classified. The UPGMA and divisive method clustered them to the west (with caribou-years in the Wabakimi Provincial Park area), Ward's method and the complete linkage methods clustered them to the east (with caribou-years in the Geraldton area) and the fuzzy *k*-means method divided the Lake Nipigon caribou-years in two-clustering half to the west (i.e., Wabakimi) and half to the east (i.e., Geraldton). To determine which cluster structure was most appropriate for classifying caribou-years in the Lake Nipigon area, we evaluated the proximity of the Lake Nipigon caribou to adjacent groups (i.e., Wabakimi and Geraldton), their general space use patterns and the relative reliability of the different clustering methods we applied.

Lake Nipigon

The seasonal median locations of Lake Nipigon caribou-years were slightly closer to those of the Wabakimi caribou-years, with an average distance of 105 km and an average minimum distance of 63 km, compared to an average distance of 113 km and an average minimum distance of 67 km in relation to the Geraldton caribou-years. The actual minimum distance between a seasonal median location of a caribou-year in the Lake Nipigon area and a caribou-year in Wabakimi was 25 km, while the shortest distance between a seasonal median location of a Lake Nipigon caribou-year and that of a Geraldton caribou-year was almost double that distance at 41 km.

All sub-sampled locations from caribou located in the general vicinity of Lake Nipigon (i.e., those assigned to either the Geraldton or the Wabakimi clusters) are displayed in Fig. 6. When the proximities of all caribou locations were compared, the average distance between locations recorded for Lake Nipigon caribou-years and those recorded for Wabakimi caribou-years was slightly higher (i.e., 123 km) than it was for Geraldton caribou-years (i.e., 110 km). However, the average and actual minimum distances between Lake Nipigon caribou-years and Wabakimi individual years were much lower than those recorded for caribou-years in the Geraldton area (i.e., 43 km and 6 km respectively, compared with 70 km and 22 km). Thus, in general, Lake Nipigon caribou appeared to be closer to caribou in the west (i.e., Wabakimi) than they were to caribou in the east (i.e., Geraldton).

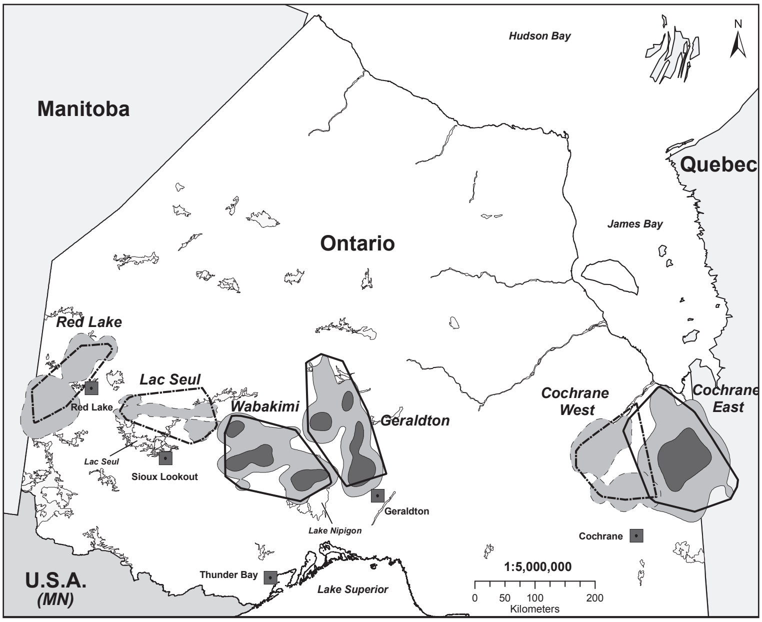

Fig. 5. Demographic unit boundaries and core areas of forest-dwelling woodland caribou (*Rangifer tarandus caribou*) at the southern limit of the ecotype's continuous distribution in Ontario. Angular polygons outlined in black represent 100% Minimum Convex Polygons generated using all the subsampled locations of the caribou assigned to each cluster. Light gray polygons represent boundaries defined using the 95% isopleth from kernel density estimates of the utilization distributions for caribou assigned to each cluster. Polygons with dashed outlines were generated using location data from a small sample of individuals. Isopleths generated using data from relatively large, broadly distributed samples of individuals have solid outlines (i.e., Wabakimi, Geraldton and Cochrane East clusters), while isopleths generated using data from a small samples of individuals have dashed outlines (i.e., Red Lake, Lac Seul, Cochrane West). Dark gray polygons represent core areas defined using the 50% isopleth from cluster-specific kernel density estimates of the utilization distribution. These core areas were only generated for clusters with large, well-distributed samples of individuals (i.e., Wabakimi, Geraldton and Cochrane East).

An evaluation of the space use patterns of the Lake Nipigon caribou suggests that these individuals were not only closer to individuals in the west, but they also made their greatest inland movements from the north-western shore of Lake Nipigon. The majority of the locations recorded for each caribou-year in the Lake Nipigon area were distributed either within the Lake (i.e., on islands or frozen lake waters) or immediately adjacent to the lakeshore (Fig. 6). The majority (i.e., 68%) of all caribou locations recorded near the eastern, north-eastern and north-central shores of the lake (n = 184) were located within 1 km of the lakeshore. The only exceptions were locations recorded on a large peninsula that extends into the lake (i.e., the North peninsula, near Ombabika Bay—Fig. 6). The 147 locations recorded near the south-western shore exhibited similar patterns—95% were located within 1 km of the shoreline and the few that were further from the lake shore were located on points and peninsulas that extended into the lake.

In comparison, in the vicinity of the north-western shore of Lake Nipigon there were several instances where Lake Nipigon caribou traveled a considerable distance inland, in the general direction of the Wabakimi caribou. Specifically, one individual spent spring of 2005 and winter and spring of 2006 approximately 5 km inland from English Bay, along the western shore of Lake Nipigon. An adult male and female that spent summers in the Ombabika Bay area along the eastern coast of Lake Nipigon, spent the late winter and spring of 2002 in a general area located approximately 8 km north-west of Windigo Bay (at distances that ranged from 5 to 11 km), on the northwest shore of Lake Nipigon. The female returned to the same general area during the winter of 2003.

An evaluation of the space use patterns of the Wabakimi and Geraldton caribou indicated that

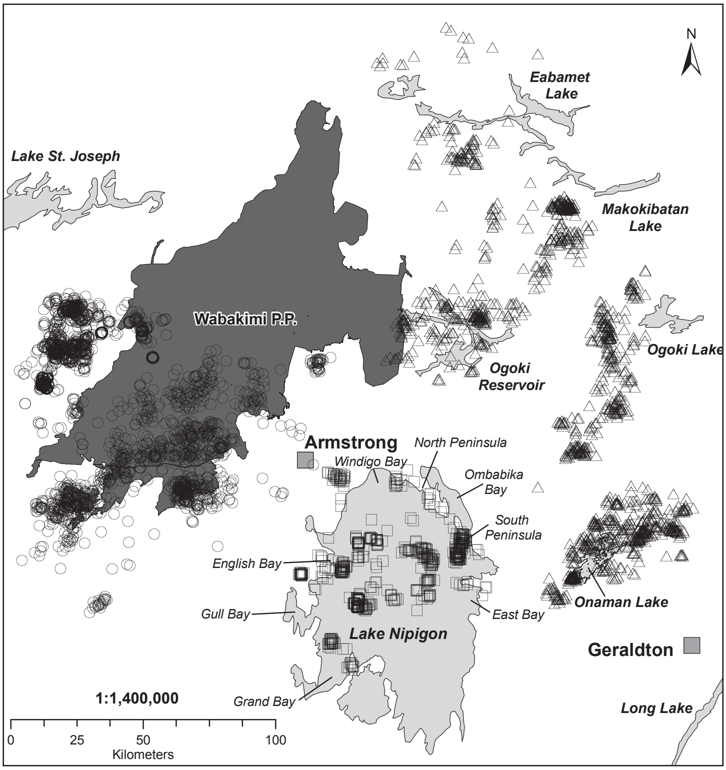

Fig. 6. Distribution of locations for collared caribou (*Rangifer tarandus caribou*) that occurred in and around the shores of Lake Nipigon (open squares) and for caribou that inhabited adjacent areas to the east (open triangles) and west (open circles). All subsampled locations recorded from 1995-2008 for individuals assigned to either the Geraldton or Wabakimi clusters are depicted. Light gray polygons represent major waterbodies. The dark gray polygon located to the west of Lake Nipigon depicts the boundaries of Wabakimi Provincial Park.

most sampled individuals from both groups did not travel closer than roughly 30 km (or more) from the Lake Nipigon shoreline. However, the nearest locations of the closest individual from each group differed considerably. Specifically, one individual from the Wabakimi area spent time in an area less than 4 km from the north-western shoreline of Lake Nipigon and the closest location recorded for a Geraldton caribou was approximately 20 km from the shoreline.

Finally, an evaluation of evidence regarding the relative reliability of different clustering methods favoured the UPGMA and divisive hierarchical methods and the fuzzy *k*-means method over Ward's and the complete linkage method (Cunningham & Ogilvie, 1972; Milligan & Isaac, 1980; Kaufman & Rousseeuw, 1990). Both Ward's and the complete linkage methods perform well when a dataset produces a spherical distribution (Kuiper & Fisher, 1975; Aldenderfer & Blashfield, 1984) but are less effective when clusters have different diameters, numerous outliers or are ellipsoidal in shape (Everitt, 1977; Aldenderfer & Blashfield, 1984; Kaufman & Rousseeuw, 1990). Since the clusters produced from our data by all methods were mostly ellipsoidal in shape (e.g., Fig. 5), the classification of the Lake Nipigon caribou-years under Ward's method and the complete linkage method were considered to be the least reliable. Consequently, given the proximity of Lake Nipigon caribou-years to Wabakimi, the presence of notable inland movements from Lake Nipigon to the north-west and the greater reliability of the methods that clustered all (i.e., UPGMA and divisive) or several (fuzzy *k*-means) of the Lake Nipigon caribou-years to the west, our results suggest grouping Lake Nipigon caribou-years with caribou-years in the Wabakimi cluster when delineating preliminary demographic units.

Cochrane

For all methods, the 6 cluster solution delineated two groups of caribou-years in the Cochrane area (i.e., east and west). However, for most methods (n=4) this distinction was not present in the 5 cluster solution. Thus, of all recognized groups, the distinction between the two Cochrane groups was the weakest. Due to the relatively low level of dissimilarity between the two Cochrane clusters and the small sample size (i.e., 5 individuals / 10 caribou-years) of the western group, we decided to look at all the location data from the Cochrane area caribou to determine whether individual space use and movement behaviour supported the distinction between groups. There was very little overlap in space use between caribou-years from the eastern and western groups. Six out of 10 caribou-years (3 out of 5 individuals) had relatively small home ranges (based on a 100% MCP), which were located in an area approximately 35 km west of the closest eastern individual. Only one wide-ranging female had ranges (n=2) that overlapped slightly with those estimated for some caribou-years in the eastern group. Given the low level of overlap and in some cases, considerable distance between home ranges of caribou-years assigned to the different groups, we decided to retain the east-west distinction in the Cochrane area when delineating preliminary demographic units.

Demographic unit boundaries and core areas

Based on the results of cluster analyses and the resolution of differences between the cluster structures delineated by different methods, each caribou-year was assigned to one of six clusters: Red Lake (*n* = 5 caribou, 8 caribou-years), Lac Seul (*n* = 6 caribou, 12 caribou-years), Wabakimi/Lake Nipigon (*n* = 21 caribou, 29 caribou-years), Geraldton (*n* = 11 caribou, 19 caribou-years) Cochrane West (*n* = 5 caribou, 10 caribou-years) and Cochrane East (*n* = 5 caribou, 10 caribou-years). The precise locations and geographic extents of each demographic unit (as delineated by the MCP and kernel density-based estimates of cluster "ranges") are depicted in Figure 5. Three clusters had relatively low sample sizes, particularly for the KDE analysis: Red Lake, Lac Seul and Cochrane East. For these clusters, only the 100% MCP and the 95% isopleth from the KDE are displayed in Figure 5. The 50% isopleths generated for the three clusters with larger sample sizes (i.e., Wabakimi, Geraldton and Cochrane East – Fig. 5) indicate that each cluster contains multiple core use areas. An inspection of the telemetry locations that fall within these core areas indicates that they represent areas that receive relatively intensive use during multiple seasons.

Demographic unit "distinctness"

In the 6-cluster solution depicted in Fig. 5, the 41 caribou collared for multiple years were assigned to the same cluster for each caribou-year included in the anlysis. This general result held true for all of the six-cluster solutions, regardless of which clustering method was applied. This lack of "cross-classification" (Taylor *et al.*, 2001) indicates that no collared caribou emigrated from one cluster to another during the study period.

While hard clustering methods assign each case (i.e., caribou-year) to a single cluster, fuzzy *k*-means clustering assigns "partial membership" coefficients, which sum to 1.00 and quantify the degree of membership that each caribou-year exhibits to all clusters delineated in a given cluster solution. Consequently, general trends in partial membership coefficient values (e.g., whether individuals generally exhibit a high degree of membership for a single cluster or whether they exhibit high coefficient values for multiple clusters) can serve as an indicator of the extent to which clusters can be viewed as distinct demographic units. For the six cluster solution obtained using the fuzzy *k*-means method, all caribou-years exhibited strong membership to a single cluster. The average maximum membership coefficient was 0.97 (standard deviation: 0.06): only 9 caribou-years had dominant membership values < 0.8 and of those, the lowest value was 0.69.

The proximity between the boundaries and core areas associated with adjacent clusters was the other major indicator of whether clusters represented demographically "distinct" groups. In general, there was very little overlap between adjacent boundaries, regardless of whether they were defined using an MCP or a kernel density estimate of range use (Figure 5; Table 1). The proportion of overlap between the boundaries of the two Cochrane ranges was 0.07 using kernel density estimates and 0.12 using MCP boundaries (Table 1). The Lac Seul and Wabakimi ranges overlapped slightly when the kernel density estimates were compared (i.e., 0.01; Table 1), but there was no overlap between the boundaries of any other adjacent range combinations.

The minimum distance between the non-overlapping boundaries of adjacent clusters varied considerably. The distance between the MCP-based boundaries of the Lac Seul and Wabakimi clusters was relatively low (i.e., 18 km; Table 1) and the minimum distance between the Wabakimi and Geraldton ranges was even lower (i.e., 12 km between MCPs and 5 km between kernel density estimates; Table 1). The minimum distance between the Red Lake and Lac Seul clusters was higher at 67 km (Table 1), and both estimates of the minimum distance between the boundaries of the Geraldton and Cochrane West clusters exceeded 300 km (Table 1).

Only one pair of adjacent clusters were considered to have sample sizes large enough to use a KDE to delineate core use areas: Wabakimi and Geraldton (Table 1). While the distance between the adjacent boundaries of these two units was relatively low, there was approximately 32 km between the closest edges of the core use areas delineated for the two ranges. This indicates that the Wabakimi and Geraldton clusters may be more demographically distinct than is suggested by boundary-based distances alone.

Demographic unit reliability

The relationship between cluster size and the number of individuals with locations included in the size estimate is depicted in Fig. 7. Rather than increasing smoothly to a single clear asymptote, the two clusters with the largest sample sizes (i.e., Cochrane East and Wabakimi) reach several prolonged plateaus

Table 1. Proportion of overlap and minimum distances between outer boundaries (100% Minimum Convex Polygon and kernel density estimate-based) and core area boundaries (kernel density estimate-based) of adjacent clusters. For situations where minimum distances between the outer boundaries of adjacent clusters may be exaggerated due to incomplete sampling, the corresponding 'Range combination' and 'Minimum distance' fields are identified by an ' * '. For clusters where available data was determined to be insufficient for obtaining reliable estimates of core use areas (i.e., Red Lake, Lac Seul and Cochrane West), core boundaries were not delineated and distances between cores are listed as 'N/A' in the table.

Range combination	Proportion of overlap		Minimum distance between cluster boundaries (km)		
	100% MCP (outer boundary)	KDE - 95% isopleth (outer boundary)	100% MCP (outer boundary)	KDE - 95% isopleth (outer boundary)	KDE - 50% isopleth (core boundary)
Red Lake & Lac Seul *	0	0	67*	55*	N/A
Lac Seul & Wabakimi	0	0.01	18	0	N/A
Wabakimi & Geraldton	0	0	12	5	32
Geraldton & Cochrane W *	0	0	315*	312*	N/A
Cochrane W & Cochrane E	0.12	0.07	0	0	N/A

when $n \geq 4$ individuals. However, the relatively small increase in cluster size from the second-last to the final plateau for Cochrane East and the prolonged length of the plateau for the Wabakimi population (from $n = 12$ to 21) indicate that sample sizes are likely sufficient for deriving accurate estimates of demographic unit boundaries and cores (EC, 2008: Appendix 6.2). Geraldton was the cluster with the third largest sample size and the relatively prolonged length of the single asymptote that it appears to reach (from $n = 5$ to 11) suggests that the existing sample size for this cluster may also be sufficient for delineating the general extent of the areas used by members of this demographic unit. In contrast, the pattern for the other three support our earlier conclusion that sample sizes are not sufficient to be considered strongly representative of demographic unit cores or boundaries.

While the Red Lake and Lac Seul clusters appear to exhibit very short plateaus when $n \geq 3$, substantial increases in cluster size could occur if more extensive sampling were conducted, as was observed for the Cochrane East and Wabakimi clusters. Additionally, the relationship between the size of the Cochrane West cluster (which has also received limited sampling effort) and number of individuals contributing locations to the estimate does not appear to have reached an asymptote, which suggests that additional sampling is needed to accurately delineate boundaries of this cluster.

Discussion

The results we obtained are significant for two major reasons. First, they demonstrate the challenges associated with delineating demographic structure, particularly when working with historic data that may not have been collected in a manner that is optimal for implementing such analyses. Second, despite the numerous limitations of the dataset, by analyzing it we gained some insight into the demographic structure of woodland caribou in Ontario. Thus, we were able to obtain information that can be used to inform pressing conservation and management decisions until more appropriate and extensive datasets are available.

The dataset: limitations and insights

The reliability of inferences about population structure that are based on spatial proximity and movement data, is dependent on the extent to which sampled individuals can be considered to be representative of the population(s) of interest. This, in turn, is a function of sampling strategy and sample size (Greenwood, 1996), as well as duration of the sampling period (EC, 2008: Appendix 6.2). The dataset analyzed here was not ideal with respect to any of these factors. For example, only the southern portion of the ecotype's range in Ontario was sampled when collecting the historic dataset and even within this region, the intensity of sampling efforts and the spatial distribution of collar deployment locations were somewhat uneven. Sample sizes were relatively high in the central and easternmost sections of the sampling region (i.e., Wabakimi = 21, Geraldton = 11 and Cochrane East = 25 individuals) and this, combined with observed asymptotes in the relationship between cluster size and the number of sampled individuals for each of these three clusters, indicates that sufficient data were available to obtain an accurate delineation of the general boundaries and core areas of local populations. In contrast, sample sizes were quite small in the western (i.e., Red Lake and Lac Seul—5 and 6 individuals, respectively) and central-eastern (i.e., Cochrane West—5 individuals) areas of the province, and no lengthy asymptotes were observed in the relationship between cluster size and the number of sampled individuals. Consequently, it was considered inappropriate to delineate cores for these areas and the boundaries delineated for these clusters should be treated as preliminary indicators of the minimum extent of demographic units.

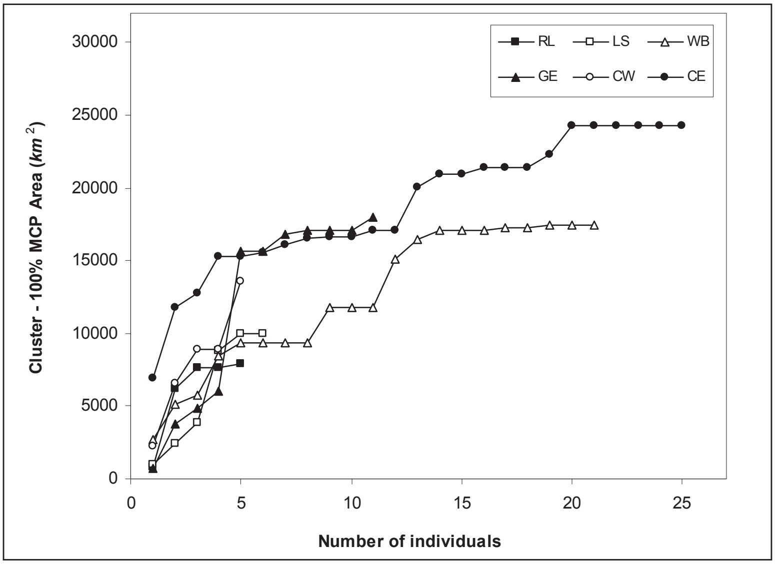

Fig. 7. The relationship between cluster size and the number of classified individuals with locations used to generate the cluster size estimate. Relationships are displayed separately for each identified cluster. The six clusters included are labeled as follows: Red Lake = “RL”, Lac Seul = “LS”, Wabakimi = “WB”, Geraldton = “GE”, Cochrane West = “CW”, Cochrane East = “CE”.

In some regions, spatial gaps in collar deployment locations appear to be representative of patchiness in the distribution of woodland caribou during the aggregative winter season (e.g., between Cochrane East and Cochrane West and in the Geraldton and Wabakimi areas). In others, these gaps reflected a lack of sampling effort (e.g., the intervening area between Cochrane West and Geraldton, and the areas between and surrounding Lac Seul and Red Lake) and they made it impossible to determine whether consequent divisions between adjacent clusters were representative of the distribution of caribou on the landscape or whether they were just artefacts of inadequate sampling. The presence of these gaps affected the cluster structure predicted under the null hypothesis (i.e., panmixia), which demonstrates the importance of identifying and accounting for sampling inadequacies when defining the clustering results expected under alternative hypotheses.

Hastings (1993) found that populations become demographically correlated when between-group migration exceeds 10% and this immigration/emigration threshold has been recommended for delineating demographic units by general (e.g., Palsbøll *et al.*, 2007) and caribou-specific sources (e.g., EC, 2008). While no between-group migration events were documented in this study, small sample sizes and the biased nature of sample composition affected the reliability of assessments of demographic distinctness based on the calculation of immigration/emigration rates. The presence of 41 individuals that were collared for multiple years made it possible to detect emigration/immigration events, but within-group sample sizes of these individuals were insufficient for calculating reliable estimates of immigration/emigration rates between adjacent groups. Additionally, evidence suggests adult female caribou exhibit a high degree of fidelity to calving sites (Fuller & Keith, 1981; Paré & Huot, 1985; Brown *et al.*, 2000; Schaefer *et al.*, 2000; but see Dyke & Manseau, 2009 for contrasting results) and, consequently, individuals in this age/sex group are probably the least likely to move from one demographic group to another. Since most sampled individuals in this study were adult females, any conclusions regarding the frequency of immigration/emigration events may be negatively biased. However, since adult female survival and reproduction are the main determinants of the population dynamics of polygynous, promiscuous species like caribou (Mysterud *et al.*, 2002; Rankin & Kokko,

2007) and their site fidelity is the factor that likely underlies spatial structuring within broader populations (Schaefer *et al.*, 2001), biased sampling in favour of this demographic group is somewhat defensible. In fact, almost all studies of large mammals that have applied similar methodologies to delineate local populations have analyzed datasets that were comprised exclusively (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Taylor *et al.*, 2001; Schaefer & Wilson, 2002; Courtois *et al.*, 2007) or predominantly (e.g., Edwards *et al.*, 2008) by adult females. Only McLoughlin *et al.* (2002) analyzed a dataset that contained similar numbers of males and females.

The limitations associated with emigration/immigration-based estimates of demographic distinctness forced us to rely on the spatial proximity of cluster boundaries and core areas as a proxy for the strength of demographic interactions between adjacent groups. Such assessments are not ideal (EC, 2008: Appendix 6.2), especially in western and central-eastern areas of the province, where small sample sizes reduce the reliability of boundary and core area estimates. However, the low degree of boundary overlap and where assessed, the relatively high minimum distances between core areas of adjacent groups, both support the emigration/immigration results and fuzzy membership coefficient results, each of which suggests that the groups delineated in this study may be relatively distinct, from a demographic perspective.

In addition to limitations associated with sample size and composition (i.e., sample dominated by single sex/age class), sampling period duration was another factor that affected the reliability of the results presented here. Environment Canada (2008: Appendix 6.2) recommended that as many as 20 continuous years of observation data be used to delineate local caribou populations, because long sampling periods are more likely to capture inter-annual variability in occupied areas and lagged responses of caribou occupancy to habitat change (e.g., Vors *et al.*, 2007). For each of the demographic units identified here, the associated sampling period was relatively short. The datasets used to delineate the Geraldton and Wabakimi units (Fig. 5) were collected over the longest time period (i.e., approximately 11 years for each area—from 1995 to 2006), but deployed collars were not evenly distributed throughout each demographic unit for the full duration of the sampling period. Sampling periods in other locations were considerably shorter: five years in Lac Seul (1995-2000), three years in Red Lake (1997-2000) and Cochrane East (1998-2001), and two years in Cochrane West (2006-2008). The short duration of sampling in most locations suggests that temporal variability in occupancy may not be well-represented in any of the 6 demographic units identified (Fig. 5). The collection of long-duration datasets (i.e., 20 years) throughout the entire study area will likely improve the ability to detect inter-annual variability and short-term changes in population structure and range boundaries. However, it is important to recognize that caribou population structure is dynamic and that current conditions may not be well-represented by historic patterns, particularly if conditions (e.g., climate, levels of natural or anthropogenic disturbance) have changed over time. For this reason, extant population structure should be re-evaluated and revised (if necessary) on a fairly regular basis (EC, 2008: Appendix 6.2).

Clearly, there is room for improvement in the dataset with respect to sample size, the distribution of sampled individuals and duration of the sampling period. Despite these shortcomings, the analysis presented here is valuable in several respects. First, it highlights the general need for more telemetry data, which can be used to obtain a comprehensive assessment of the number, extent and demographic distinctness of local populations of woodland caribou in Ontario. A formal analysis of telemetry data isn't the only approach available for determining the extent of local populations—alternatives include genetic analyses, the collation of long-term incidental or survey sightings or the use of Traditional Local Knowledge (EC, 2008: Appendix 6.2). Of these, only genetic analyses share the major advantages of telemetry-based analyses. Namely, both approaches can include standardized, objective methodologies for delineating demographic structure and both allow researchers to draw inferences about the level of individual movement between local populations, which is essential for calculating immigration/emigration rates.

Many standard population genetic methods provide genetic divergence estimates that are averaged over recent evolutionary time and may not be indicative of current rates of gene flow (Palsbøll *et al.,* 2007). This can diminish the value of genetic data as a source of information regarding current (vs. historic) demographic structure (Avise, 1992; Cronin, 1993; Moritz, 1994). However, recent developments in molecular ecology allow genetic data to be used to derive dispersal rate estimates that apply to recent generations (Palsbøll *et al.,* 2007). The latter approaches can be applied to determine whether effective dispersal between groups falls above or below the 10% threshold (Palsbøll *et al.,* 2007; EC 2008: Appendix 6.2) and thus, they can be very useful for delineating meaningful demographic units (e.g., Ball *et al.,* 2010). Therefore, genetic analyses can provide insights into demographic structure that complement the information provided by telemetry-based analyses like the one presented here. A combined consideration of individual movements and population genetic data will likely produce a more comprehensive picture of demographic structure than singular reliance on either type of evidence would (e.g., Boulet *et al.*, 2007) and thus, we recommend that further efforts be undertaken to collect and analyze both types of data.

Extensive efforts to collect more caribou telemetry data are currently underway within Ontario (G. Racey, OMNR, pers. comm., 28 May 2010) and the results presented here can provide detailed insight into how and where data collection should proceed. Specifically, more sampling is needed throughout the northern portion of the ecotype's range and in specific sections of the southern portion of the range (i.e., the western and central-eastern sections) to achieve an even distribution of sampling effort throughout the study area (Schaefer *et al.,* 2001) and to ensure that collar deployment locations are representative of the distribution of animals on the landscape. Additionally, longer-term sampling should be considered throughout the entire extent of forest-dwelling woodland caribou range, in order to capture temporal variability in space use. Finally, efforts to increase sampling amongst age/sex classes that have been poorly represented in earlier studies (i.e., adult males and reproductively immature individuals of either sex) should also be considered, as the movements of these individuals may be less constrained by fidelity to specific locations (e.g., calving sites).

The second major contribution of this study is the preliminary insights it provides into the demographic structure of forest-dwelling woodland caribou at the southern edge of their continuous range in Ontario. Specifically, the results presented here support the existence of demographic structuring within the ecotype's continuous range in northern Ontario. The delineation of the Red Lake group and the separation between the Cochrane clusters and the caribou in the central part of the province could just be artefacts of insufficient sampling efforts. However, the cluster results, in combination with an assessment of the representativeness of collar deployment locations, provide support for three additional demographic distinctions: between Cochrane East and Cochrane West, between Geraldton and Wabakimi and between Wabakimi and Lac Seul.

Several lines of evidence suggest that these spatial clusters of caribou represent demographically distinct local populations. These include (1) the high degree of similarity (i.e., in cluster solution size and composition) across cluster methods, (2) the strong membership that each caribou-year exhibited towards a single cluster (as indicated by fuzzy membership coefficient values), (3) the lack of migration between clusters amongst caribou collared for multiple years, (4) the low level of overlap between the boundaries of adjacent clusters and (5) where it was possible to measure, the considerable distance between core use areas associated with adjacent groups. In the end, evidence in favour of multiple demographic units in our study is stronger than that presented by several other studies that claim to delineate population structure, in terms of between-method consistency in results (e.g., Schaefer *et al.,* 2001), the degree of overlap between adjacent clusters (Bethke *et al.,* 1996; Schaefer *et al.,* 2001; Edwards *et al.,* 2008) and immigration/emigration rates (Schaefer *et al.,* 2001; Taylor *et al.,* 2001).

While this evidence does support the presence of demographic structuring, the level of discreteness between adjacent units appears to be relatively low. Short distances between cluster boundaries (relative to home range size), inconsistency in the classification of the Lake Nipigon caribou and the low density of natural and anthropogenic barriers between delineated units indicates that the distribution of caribou throughout the study area may be relatively continuous at a coarse scale. However, the evidence described above is consistent with the existence of geographic clusters of animals with dynamics that are more likely to be influenced by interactions with each other than with members of adjacent groups.

The resources and costs associated with collecting a telemetry dataset that is ideal for population delineation are very high and available funds are often likely to fall short of what is needed. Additionally, even with adequate resources, considerable time would be required to address some of the weaknesses outlined above (e.g., short sampling periods). In the meantime, decisions regarding natural resource extraction and infrastructure development continue to be made in the regions of Ontario that are currently occupied by caribou. As long as the uncertainties associated with the demographic units delineated in this study are explicitly recognized, they can be used to inform land use planning decisions and development and implementation of conservation and recovery strategies for woodland caribou. Relevant policies, plans and guidelines can be adjusted when better data become available.

Levels of organization

The methodological approach that we applied here was based on several earlier studies of various species which analyzed individual locations to identify distinct demographic groups and delineate their boundaries. Most of these focused on large, wide-ranging temperate and arctic-dwelling mammals such as polar bears (*Ursus maritimus*) (e.g., Bethke *et al.*, 1996; Taylor *et al.*, 2001), grizzly bears (*Ursus arctos horribilis*) (e.g., McLoughlin *et al.*, 2002; Edwards *et al.*, 2008) and woodland caribou (e.g., Schaefer *et al.*, 2001; Schaefer & Wilson, 2002; Courtois *et al.*, 2007). Despite the high degree of similarity in methodologies and study organisms, the spatial extent of study areas differed greatly among these studies.

Some studies analyzed datasets that spanned relatively broad areas: 900 km by 350 km (Bethke *et al.*, 1996), 3000 km by 1000 km (Taylor *et al.*, 2001), 1500 km by 1000 km (Schaefer & Wilson, 2002) and 1200 km by 300 km (this study). One study analyzed data collected from more moderately-sized areas (i.e., 450 km by 400 km; McLoughlin *et al.*, 2002), while several others have analyzed data from relatively small study areas: 250 km by 200 km (Schaefer *et al.*, 2001), 300 km by 250 km (Courtois *et al.*, 2007) and 150 km by 250 km (Edwards *et al.*, 2008). Sample sizes amongst these studies ranged from 26 to 131 individuals (average = 69, standard deviation = 36) and there was no apparent relationship between sample size and the size of the study area. Additionally, the number of clusters delineated was similar among studies (average = 4, standard deviation = 1.5), but there was no relationship between the size of study area and cluster number.

Even though there is extensive variation in both study area size and the "sample size-to-study area size" and "study area size-to-cluster number" ratios, all of the studies listed above interpret delineated groups as representing sub-populations that are embedded in larger metapopulations (e.g., Bethke *et al.*, 1996; Schaefer *et al.*, 2001; Courtois *et al.*, 2007; Edwards *et al.*, 2008). However, given that many ecological patterns and processes vary across scales (Wiens, 1989; Schaefer, 2006), it seems likely that the demographic units identified by studies conducted at widely divergent spatial extents represent different levels of spatial organization. The universal application of the "subpopulation" label amongst these studies probably stems from the common characterization of populations as operating at two basic spatial scales: regional and local (i.e., metapopulations and subpopulations) (Schaefer, 2006). This perspective is illustrated in the discussion that Edwards *et al.* (2008) provide regarding the identification of ecologically meaningful scales for conservation and management. However, despite its widespread use, Schaefer (2006) suggests that this two-tier spatial characterization is an over-simplification of population structure and processes, which likely exist at multiple, nested scales.

Allowing for the possibility of more than two levels of population structure seems especially appropriate for forest-dwelling woodland caribou. While they are relatively solitary during and after calving (Bergerud *et al.*, 1990; Schaefer *et al.*, 2001; Ferguson & Elkie, 2004a), they tend to form relatively small groups of individuals during autumn and/or winter (Shoesmith & Storey, 1977; Darby & Pruitt, 1984; Brown *et al.*, 1986; Stuart-Smith *et al.*, 1997; Rettie & Messier, 1998; Brown *et al.*, 2000; Ferguson & Elkie, 2004a). While aggregations of up to 80 individuals have been documented in Ontario during the winter months (Cumming & Beange, 1987), average group sizes have been estimated at less than 10 individuals (Cumming & Beange, 1987; Bergerud *et al.*, 1990). Given the small size of these groups or "bands" (Cumming & Beange, 1987), they are probably best understood as nested subsets of larger subpopulations, which are themselves embedded in broader-scale metapopulations. Cumming and Beange (1987) even suggest that the large aggregations that are occasionally observed are comprised of multiple bands and thus represent an additional level of organization, intermediate between autumn/winter "bands" and subpopulations.

Most of the studies that document group formation during autumn note the association between aggregation and rutting activities (e.g., Bergerud, 1973; Shoesmith & Storey, 1977; Fuller & Keith, 1981; Paré & Huot, 1985; Rettie & Messier, 1998). There is little evidence regarding the rigidity of caribou "band" membership across years and seasons, but that which exists indicates that there may be considerable fluidity in group membership over the autumn-winter period (Bergerud, 1973; Brown *et al.*, 2000) or between years (Paré & Huot, 1985). However, if these groups are at least partially comprised of inter-breeding pairs or closely related individuals (parent-offspring) and/or they share similar experiences (e.g., shared resources or conditions) that cause their vital rates to differ from those of other groups in the subpopulation, then even this finest level of organization may be significant from a demographic perspective.

Since it seems likely that caribou population structure exists at multiple spatio-temporal scales, with spatial and demographic affinities that decline at higher hierarchical levels, some consideration should be given to determining what level of organization is represented by the groups delineated in this study. An inspection of the 100% MCPs generated for each individual (not shown here) reveals that with the exception of Cochrane East, each demographic unit is comprised of multiple groups of individuals (i.e., with highly overlapping home ranges) that are spatially distinct (exhibiting little to no overlap) from other groups. These patterns of individual space use, in combination with the large cluster size (i.e., average = 14 684 km^2, standard deviation = 5699 km^2, for 100% MCPs for each cluster), suggests that the demographic units delineated here correspond with subpopulations that are nested within a broader metapopulation which, in some cases may be comprised of multiple, smaller spatially distinct groups (e.g., the "Wabakimi" cluster and the "Geraldton" cluster – Figure 6). This finest level of organization may occur if significant natural or man-made disturbances temporarily restrict caribou movements (G. Racey, OMNR, pers.comm., 29 Nov. 2010) or if space use is bounded by strong individual selection for static geographic features (e.g., large lakes or peatland complexes).

Management implications

The range retractions and population declines exhibited by the boreal population of forest-dwelling woodland caribou have resulted in its designation as a conservation priority at national and provincial/territorial levels (Thomas & Gray, 2002; EC, 2008; OMNR, 2009). Consequently, in the jurisdictions that overlap the organism's extant range, there have been several recent efforts to develop woodland caribou conservation and recovery strategies (e.g., MC, 2005; MRNFQ, 2008; OWCRT, 2008; OMNR, 2009).

Efforts to incorporate habitat-based considerations when delineating "units of analysis" can aid in designing conservation strategies that avoid fragmenting continuous areas of caribou range (EC, 2008: Appendix 6.2). However, conducting status assessments using data collected over broad geographic areas could mask local variation within the larger range, which could result in unexpected local extirpations and range loss (EC, 2008: Appendix 6.2). Thus, consideration of existing population structure is also critical for delineating meaningful "units of analysis" for the boreal population of woodland caribou. One option for effectively integrating both types of information (i.e., habitat and population structure) would be to prioritize large, habitat-based ranges when developing and implementing recovery strategies, while local populations (defined based on caribou space use and movement) could be used as the primary units of analysis for calculating vital rates and assessing population viability (e.g., Arsenault *et al.* 2003) or the cumulative impacts of anthropogenic disturbance (e.g., Sorensen *et al.* 2008). While implementing the second component (i.e., local population delineation) of this option, it is important to remember both the dynamic nature of caribou population structure and that major changes in caribou occupancy patterns and demographic connections may occur over relatively long time periods (i.e., multiple decades). Consequently, results like those presented here can only provide insight into caribou population structure and occupancy over a discrete period of time. As such, they should be viewed as one of several "snapshots" of population structure that will likely be produced over the course of a long-term adaptive management cycle (EC, 2008: Appendix 6.2; OMNR, 2009).

We did not conduct a formal assessment of the spatial distribution of caribou habitat. However, because the study area is located at the northern limits of commercial logging in Ontario and there are no large communities, extensive permanent developments, or impenetrable geographic boundaries located between the demographic units delineated here, it seems likely that caribou currently occur within relatively continuous habitat. Subsequently, the boundaries of demographic units identified by the methods we have described should be considered when assessing population or range status.

The same general approach for incorporating the information obtained from a telemetry-based analysis of population structure into management can also be used to determine how to deal with the two locations where the determination of demographic unit boundaries was uncertain. The caribou in the Lake Nipigon area were the only individuals with cluster assignments that differed between methods. An evaluation of additional evidence supported grouping them with individuals to the west when delineating population boundaries and core areas. However, the discrepancies between cluster results and the lack of overlap in space use between Lake Nipigon caribou and individuals to the east and west, suggests that considerable uncertainty remains regarding the appropriate classification of these individuals.

A management strategy that explicitly accounts for this uncertainty would assess population viability based on the area of occupancy associated with the Lake Nipigon individuals, while recovery efforts could focus on maintaining or restoring habitat in the intervening landscape between Lake Nipigon and caribou in the Wabakimi and Geraldton areas. With respect to the recovery effort component, such an approach is supported by historic evidence for the movements and seasonal occupancy patterns of Lake Nipigon caribou, which supports demographic connections with groups to the west (Cumming & Beange, 1987; Bergerud *et al.*, 1990) and east (R. Hartley, OMNR, pers. comm., 2 Dec. 2010).

Additionally, more recent evidence of caribou occurrences in the inland areas adjacent to Lake Nipigon (obtained using other survey methods), suggests that these connections may still persist to some degree (G. Racey, OMNR, pers. comm., 29 Nov. 2010). Finally, until further data are available that enables the relationship between the two groups in the Cochrane West and Cochrane East areas to be defined with greater certainty, a similar management approach could be applied in this area of the province. Namely, population viability assessments could be based on the boundaries of the Cochrane East and Cochrane West units and recovery efforts could account for the potential connections between these adjacent groups.

Delineation of "critical" habitat for woodland caribou in Ontario and elsewhere should be based primarily on analyses that identify the resources and conditions associated with occupancy (e.g., by applying Resource Selection Functions - Manly *et al.*, 2002). Undertaking such analyses was beyond the scope of this paper. However, the results of the kernel density estimation analysis provided some insight into areas that could be important from a caribou conservation and management perspective.

There was distinct variation in the intensity of caribou use in each of the three clusters that had sufficient data to generate 50% isopleths (i.e., Wabakimi, Geraldton and Cochrane East). Each cluster contained one or more "core" areas of intensive use, with evidence of some level of occupancy throughout the year.

Resource Selection Functions (RSFs) or other formal analyses of habitat selection would be required to test alternative hypotheses regarding the mechanistic basis for variation in the intensity of use in each cluster and to enable comprehensive mapping of probability of caribou use across the sampled portions of the study area. However, for a variety of reasons (e.g., inadequate characterizations of explanatory variables, metapopulation dynamics – Hanski & Simberloff, 1997), RSF-based probabilities of use may not always correspond with existing patterns of occupancy. Consequently, the geographic areas with high levels of historic caribou use identified here should be considered in conjunction with RSFs to delineate locations that may play an important role in the persistence of local caribou populations. Managers might consider prioritizing these areas for short or long-term conservation efforts, depending on how temporally dynamic the associated resources, conditions or processes that promote caribou occupancy are likely to be.

An evaluation of the characteristics associated with relatively low and high levels of use could also provide insights into which resources and conditions might be producing caribou occupancy and consequently, which environmental correlates may need to be included or improved when generating RSF-based definitions of critical habitat. Finally, the spatial discreteness of core areas within and between clusters and the existence of several areas that are characterized by relatively low probabilities of occupancy, suggests that while caribou are present across much of the sampled portion of the study area, the intensity of caribou use across this broad region may vary considerably. This variation in caribou occupancy should be taken into account when estimating effective range sizes or deriving coarse population estimates.

Until additional data are available for analysis, only provisional conclusions can be drawn about the population structure of woodland caribou at the southern margins of their continuous range in Ontario. While this information can and should be considered when making imminent management decisions, the limitations of the historic dataset and the preliminary nature of the results presented here should not be forgotten. Any future initiatives designed to obtain further information on the demographic structure of caribou in Ontario or elsewhere, should include concerted efforts to ensure that (1) sampling efforts are uniform, (2) collar deployments are representative of the distribution of caribou throughout the study area and (3) the spatio-temporal resolution and extent of the telemetry data are appropriate for capturing spatial population structure and temporal variation in caribou movements. Definitive telemetry-based assessments of population structure are not possible without such datasets.

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