

# Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*)

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## Abstract

For species conservation, defining seasons according to an animal's perception and consideration of seasonal differences in its use of space is required. First, a statistical approach was used to determine seasons based on rates of movement of radio-collared caribou *Rangifer tarandus caribou*. Using polynomial regression, five seasons were delineated by inflection points that demarcate changes in rates of movement. Male and female caribou did not differ in timing and number of seasons. Second, the seasons so defined were used to describe the use of space in 33 caribou in north-western Ontario, Canada. Greatest rates of movement occurred during spring and early winter migration when caribou had both the largest range size and largest distance between seasonal ranges. The general direction of movement was west in spring and east early in winter, although variation occurred among caribou and years. A drop in rate of movement lasting about 3 days may indicate calving. Caribou were most dispersed and occupied the smallest seasonal range during the calving season. The animals showed strong fidelity to calving areas in contrast to the highly variable year-to-year location of winter ranges. Understanding the seasons of animal movement patterns, and applying this understanding when developing plans for forest management, may help reduce adverse effects of forest harvesting on highly mobile animals such as woodland caribou.

**Key words:** dispersion, forest management, home range, migration, predation, *Rangifer tarandus caribou*, wolves

## INTRODUCTION

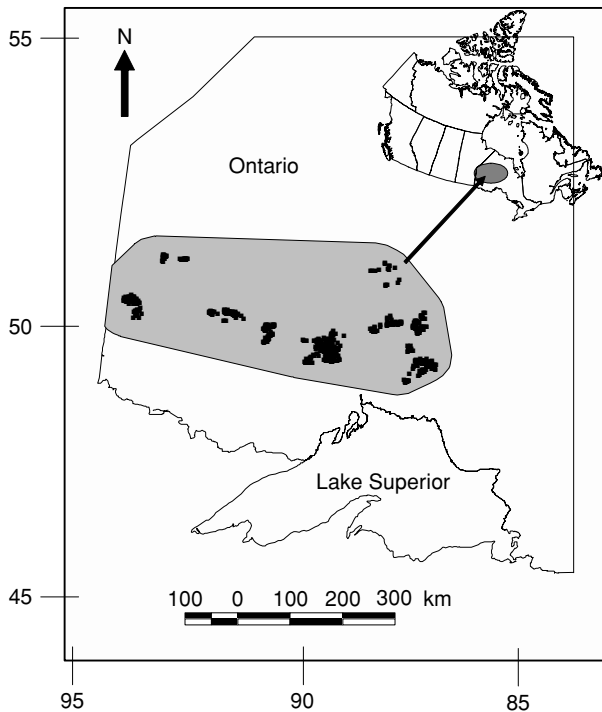
Conservation of highly mobile animals is aided by an understanding of their use of space. Predation is the main proximate factor of population limitation of woodland caribou *Rangifer tarandus caribou* Gmelin across North America (Bergerud, 1974; Seip, 1992) and caribou have evolved dispersal strategies to minimize it (Ferguson, Bergerud & Ferguson, 1988; Bergerud, Ferguson & Butler, 1990; Caughley & Gunn, 1993). Caribou move across the landscape season by season both to reduce predation (Bergerud & Page, 1987; Stuart-Smith *et al.*, 1997) and to obtain seasonally available food (Rettie & Messier, 2000; Johnson, Parker & Heard, 2001). Woodland caribou are thought to minimize the risk of predation by avoiding other ungulates such as moose *Alces alces*, which are the main food of wolves *Canis lupus* (Bergerud, Butler & Miller, 1984; Seip, 1991). In some boreal regions, female caribou leave their wintering grounds during the spring migration and move to calving areas where lakeshores, islands or bogs (Bergerud, 1985; Cumming & Beange,

1987; Valkenburg *et al.*, 1996; Stuart-Smith *et al.*, 1997) provide refugia from wolves and bears *Ursus* spp.

Woodland caribou also move from summer habitat to a winter landscape characterized by mature conifer cover that provides arboreal lichen (Terry, McLellan & Watts, 2000; Johnson *et al.*, 2001) and a landscape pattern that reduces the risk of wolf predation (Carruthers *et al.*, 1986). With increasing economic development of boreal forests (Vistness *et al.*, 2001), there is a pressing need to know how highly mobile animals such as caribou move among different seasonal habitats to avoid predators and obtain food. Such basic information as seasonal rates of movement, spatial and temporal segregation of sexes, migration direction, and fidelity are necessary to address conservation issues related to the threatened status of woodland caribou in Canada.

Telemetry information from 33 collared caribou collected from 1995 to 2000 was used to study the patterns of caribou movements in a boreal landscape. The 160 000 km<sup>2</sup> study area ranges across north-western Ontario from the Manitoba border in the west to the western edge of the Hudson Bay lowlands in the east. First, we defined different seasonal phases of movement in caribou using a statistical approach based on changes in rates of movement. Here, we define phase shifts in the

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**Fig. 1.** Location of study area and woodland caribou *Rangifer tarandus caribou* locations within north-western Ontario, 1995–2000.

movement behaviour of caribou as ‘seasons’, which differ from conventional climatic seasons. Next, we described seasonal movement patterns according to seasonal range size, dispersion, and fidelity to particular areas. We then tested for differences in seasonal and annual range shifts. Last, we described the direction of seasonal movements. Our goal was to delineate seasons of woodland caribou and compare characteristics of space use, such as dispersion and fidelity, among these seasonal ranges.

## METHODS

### Study area

The study area lies between 49°30′N and 53°00′N and 87°00′W and 95°30′W and is largely within the Boreal Ecoregion of Ontario (Fig. 1). This area consists of jack pine *Pinus banksiana* Lamb. dominated forests with black spruce *Picea mariana* (Mill.) B.S.P., balsam fir *Abies balsamea* (L.) Mill., white spruce *P. glauca* (Moench) Voss, white birch *Betula papyrifera* Marsh., and trembling aspen *Populus tremuloides* Michx. on rolling rocky uplands with coarse well-drained soils (Rowe, 1972). The natural wildfire cycle in the area is between 60 and 200 years (Li, Ter-Mikaelian & Perera, 1996). Till deposits composed of coarse soils are common in the study area. Bedrock outcrops are also common, where parent materials were washed away or removed by glaciers (Baldwin, Desloges & Band, 2000).

The climate is humid continental with a mean minimum January temperature of  $-25^{\circ}\text{C}$  and a mean maximum daily temperature for July of  $23^{\circ}\text{C}$  (Baldwin *et al.*, 2000). Mean annual precipitation is 650–800 cm, including a mean January snowfall of 55 cm (Baldwin *et al.*, 2000).

Other ungulates in the region included moose and white-tailed deer *Odocoileus virginianus* (Dobbyn, 1994). Large carnivores in the area include wolves *Canis lupus*, coyotes *Canis latrans*, black bears *Ursus americanus*, wolverines *Gulo gulo*, and lynx *Lynx canadensis* (Dobbyn, 1994).

### Capture and radio-collaring

Caribou were captured using net guns in winter ( $n = 19$ ) and while swimming in summer ( $n = 14$ ) and they were equipped with both satellite (UHF) and VHF transmitters (Telonics, Inc., Mesa, AZ, U.S.A.). Eleven radio collars were deployed on caribou in 1995, 5 in 1996, 11 in 1997, and 5 in 1998, for a total of 27 female and 6 male caribou with 10 collars redeployed. Animal capture and handling procedures followed the approved protocol of the Ontario Provincial Animal Care Committee (No. 01–27).

### Locations

Radio-collared caribou transmitted ultrahigh frequency (UHF) signals from 5 March 1995 to 24 April 2000 providing information over a 6-year period. The original 11 354 UHF locations were reduced to 5201 by selecting only high accuracy locations (class > 0; location accuracy < 1 km; Service Argos, 1988) and only the highest quality location per day. Satellite transmitters were programmed to transmit for 8-h periods every 2 days from 15 March to 1 June and from 15 October to 15 January, and for 8-h periods every 7 days from 2 June to 14 October and from 16 January to 15 March. Locations were examined for outliers by calculating angular movements that identified erroneous locations (Keating, 1994; Ferguson & Elkie, in press).

### Delineation of seasons

The following analyses were done separately for males and females. First, the effect of differences in time between locations were removed. Movement rate is influenced by the interval between successive successful locations (Ferguson, Rettie & Messier, 1998), which varied in our study from 2 to 10 days. To control for this, we used log-linear regression to model the increase in distance with greater time (up to 10 days) and then used the residuals from this relationship in subsequent analyses:

$$\ln(\text{distance} + 0.5) = m * \ln(\text{time}) + c + \varepsilon$$

so that:

$$\text{distance} = \text{time}^{m*} e^{c+\varepsilon}$$

We were interested in determining when animals moved from summer to winter range and from winter to

summer range and the changes in rates of movement that would delineate the migratory seasons. First, the residuals of distance moved ( $n = 5201$ ) were modelled from the previous analysis against Julian day (day) using polynomial regression that varied the number of terms from 1 to 11 to assess the best fit model:

$$\text{residuals} = (\text{day})^1 + (\text{day})^2 + (\text{day})^3 + (\text{day})^4 + \dots \\ + (\text{day})^{11} + c + \varepsilon$$

Movement seasons were expected to be delineated by the inflection point (i.e. second order derivative = 0), which indicated a change in movement rate (km/day) from positive to negative or negative to positive and thereby demarcated the beginning or end of any seasons (e.g. Skogland, 1988; Ferguson, 2002). A plot of the explained variation ( $r^2$ ) against the number of polynomial regression terms was inspected to visually identify a minimum number of terms that adequately described the observed relationship (i.e. asymptotic plateau in the number of terms). The regression was run 3 times, once with all caribou (males and females) and then with only female and then only male caribou. Qualitatively the 2 models did not differ; therefore we report the pooled results with the larger sample size. However, for calving date determination we relied only on the female caribou model.

### Seasonal range size, dispersion, distances, and direction

Seasonal range was defined as the 100% minimum convex polygons (Jennrich & Turner, 1969) of caribou telemetry locations because this method has the fewest assumptions related to how the areas are used by animals and because it works reasonably well with small sample sizes. The seasonal range encompassed the locations of an animal during each season and was calculated using Animal Movement extension for ArcView (Environmental Systems Research Institute, Hodge & Eichenlaub, 1997); 100% minimum convex polygons from which outliers had already been removed were used. Average dispersion was estimated using a FORTRAN program that calculated the average distance between all combinations of locations within a season (Conner & Leopold, 2001). Distances between successive seasons were calculated for each caribou using centre points for seasonal location data. Also, we calculated distance from late winter to summer calving ranges. To assess seasonal range fidelity for caribou observed for > 1 year, the distance between successive centre points for each season was measured from year-to-year. Centre points were geometric means calculated from the minimum convex polygons.

Directions of travel (azimuths) between successive seasons were calculated for individual caribou and expressed using frequency data within 8 45° categories (337.5–22.4, 22.5–67.4, 67.5–112.4, 112.5–157.4, 157.5–202.4, 202.5–247.4, 247.5–292.4, 292.5–337.4) that corresponded to ordinal directions (north, north-east, east, south-east, south, south-west, west, north-west). The

mean angle and 95% confidence interval were calculated according to Zar (1996).

### Statistical analyses

Movement data were not normally distributed and transformations (e.g. log, arc-sine) failed to improve normality (Wilk's Shapiro normality test). Therefore, ranked data in general linear models (i.e. nonparametric ANOVA; Conover & Iman, 1981) was used. Interactions were not investigated, as interactions are meaningless in analyses using ranked data (Seaman *et al.*, 1994). All  $F$  and  $P$  values are reported from ranked general linear models; however, statistical analyses were re-run using unranked data to provide least-square means for presentation of data.

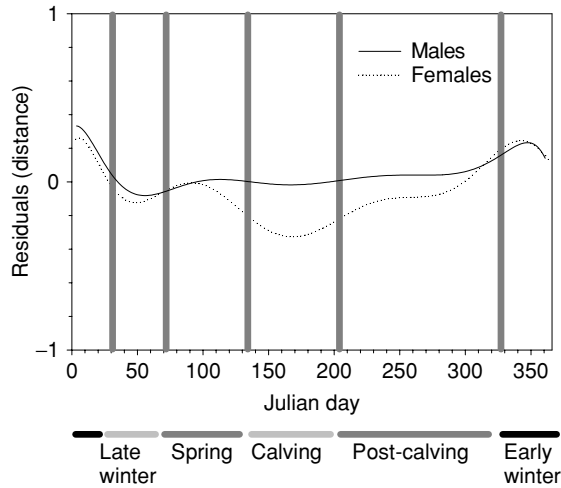
To compare the male and female models of movement over time, the Kolmogorov–Smirnov (K–S) test was used to compare the statistical differences in distributions.

Analysis of variance of ranked data was used to compare the following movement measures among seasons: movement rate, distance moved, seasonal range size, dispersion, distance between seasons, and distance between successive years. Comparison in movement rate and distance moved across seasons are provided for descriptive purposes as these measures were used to delineate seasons and consequently were expected to differ. The number of locations, sex, and individual caribou were expected to influence all of these measures of movement. Therefore, we included these fixed effects in an initial multiple ANOVA of ranked values. Results did not differ in any of the analyses of variance tests between the 6 males and 27 females ( $F_{4,247} = 0.18\text{--}0.25$ ,  $P = 0.44\text{--}0.84$ ) and there was no interaction effect between sex and season ( $F_{2,247} = 0.09\text{--}0.21$ ,  $P = 0.67\text{--}0.98$ ). Least-square means by season are reported in the Results to control for variation owing to sampling bias, sex, and individual caribou effects. Where sample size (number of locations), sex, and individual caribou effects were not significant, however, the analysis was re-run and the results of a 1-way analysis of variance of ranked data reported. Tukey's test was used to distinguish differences in multiple comparisons among seasons. Results are reported as untransformed mean  $\pm$  SE to provide comparisons with other research results. Data were analysed using SAS statistical software for microcomputers (SAS, 1989).

## RESULTS

### Delineating seasons

Distance moved was positively related to days between telemetry observations ( $F_{1,3950} = 52.4$ ,  $P = 0.0001$ ,  $r^2 = 0.413$ ). The  $\ln(\text{distance})$  versus  $\ln(\text{day})$  relationship was represented by a regression with slope  $< 1$  (0.419) indicating a fractal pattern of non-linear increase in movement rate with days between location dates. To



**Fig. 2.** Phases of male and female woodland caribou *Rangifer tarandus caribou* based on rates of movement for five seasons.

control for this bias the residuals from the log-log linear regression of days against distance were used in the following analysis.

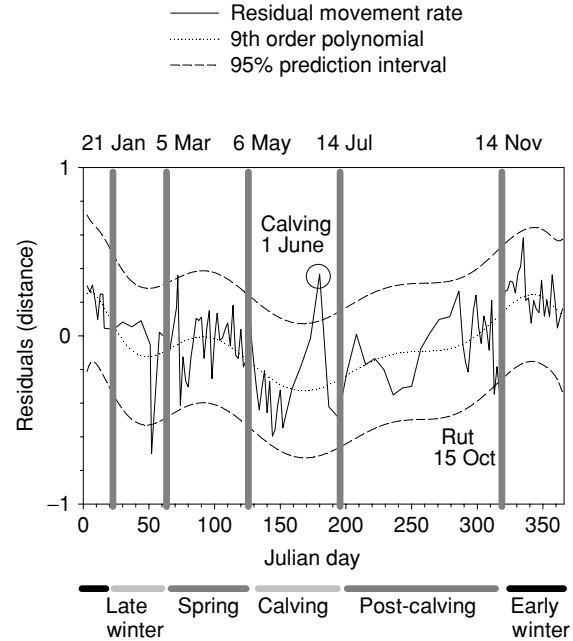
Phases using residuals of distance moved against Julian days fitted to a polynomial regression were estimated separately for each sex (Fig. 2). Season start–end dates varied by < 8 days between male and female models. Also, the models for males and females did not differ significantly in distribution ( $K-S_a = 1.40, P = 0.64$ ). Therefore, data were combined for both sexes for subsequent analyses.

For combined males and females, an asymptote in variance explained ( $r^2$ ) occurred from the 9th order polynomial through the 11th order indicating a threshold of explained variance. Therefore, we chose to use the 9th order polynomial model to delineate seasons:

$$\begin{aligned} \text{residuals} = & 0.218(\text{day})^0 + 0.0175(\text{day})^1 \\ & - 2.07 \times 10^{-3}(\text{day})^2 + 6.08 \times 10^{-5}(\text{day})^3 \\ & - 8.37 \times 10^{-7}(\text{day})^4 + 6.33 \times 10^{-9}(\text{day})^5 \\ & - 2.79 \times 10^{-11}(\text{day})^6 + 7.13 \times 10^{-14}(\text{day})^7 \\ & - 9.83 \times 10^{-17}(\text{day})^8 + 5.64 \times 10^{-20}(\text{day})^9; \\ & r^2 = 0.411, \end{aligned}$$

where residuals is the residual distance moved calculated from least-squared regression of distance versus time; (day) = Julian day, where Julian day 1 = 1 January.

Five phases were identified from the inflection points: (1) late winter from 21 January to 5 March; (2) spring from 6 March to 6 May; (3) calving from 7 May to 14 July; (4) post-calving from 15 July to 14 November; (5) early winter from 15 November to 20 January (Fig. 3). A sixth season was partially delineated within the post-calving period; however, this season was judged to be less distinct (< 1 SE difference) than the other five seasons (Fig. 3) and therefore it was not considered further.



**Fig. 3.** Seasons of woodland caribou *Rangifer tarandus caribou* determined from differences in second derivative of log–log-linear regression of distance (km) on time (day):  $\ln(\text{distance}) = m \cdot \ln(\text{time}) + c + \varepsilon$ . Horizontal grey bars, inflection points (second derivative = 0) from 9th order polynomial that demarcate season start/end.

For the female only data, a spike in movement rate (1.1 km/day) suggested a calving date of 1 June (Fig. 3). This possible mean parturition date was represented by a movement of > 500 m about 6 days before 1 June followed by a brief (*c.* 3 day) sedentary period of low movement rate (0.2 km/day).

### Seasonal rates of movement, range size, and dispersion

Sample size (number of locations per animal season) and individual caribou, but not sex, affected rates of movement. Individual collared caribou provided 23–312 locations across 3–16 seasons with the number of locations varying from three to 17 for any given season. Larger number of locations within a season resulted in an estimation of greater rates of movement ( $F = 49.5, P = 0.0001$ ), and rates varied among individual caribou ( $F = 4.4, P = 0.0001$ ). However, males and females did not differ significantly in rates of movement ( $F = 0.09, P = 0.77$ ). No effect owing to sample size, sex, or individual caribou affected results for seasonal range size, dispersion, distances, and direction; therefore only the one-way analysis of variance results are reported.

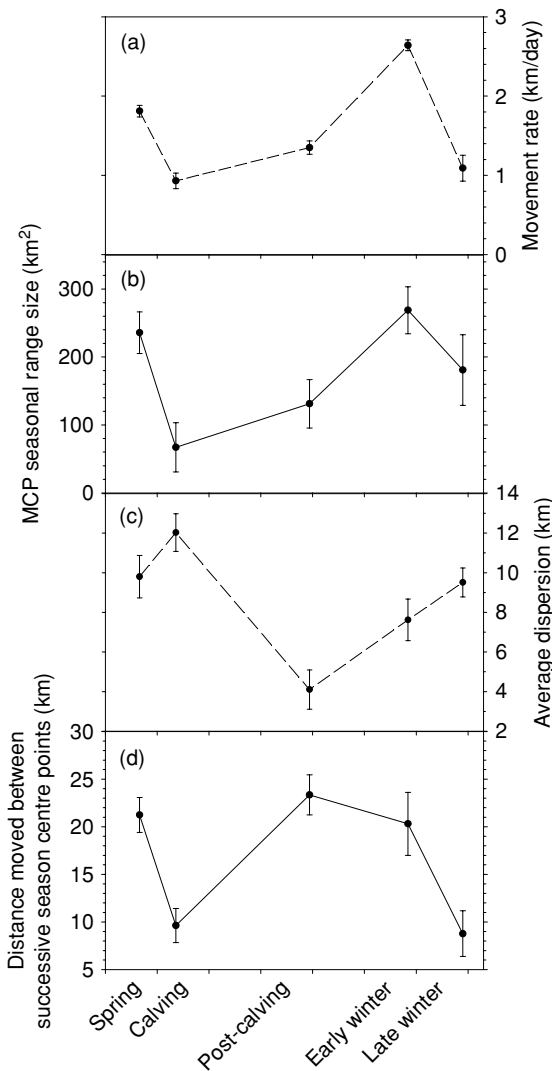
Movement rate was greatest for early winter (2.5 km/day) and spring (1.8 km/day) relative to late winter (0.9 km/day), calving (1.1 km/day), and post-calving (1.3 km/day; Table 1). This comparison identified spring and early winter as the migration seasons (Fig. 4a).

Range size varied with seasons ( $F_{4,247} = 6.91, P = 0.0001$ ). Largest ranges occurred for spring and early

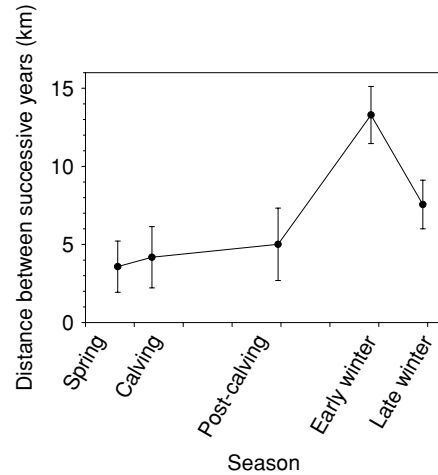
**Table 1.** Differences in movement rate among seasons for woodland caribou *Rangifer tarandus caribou* in north-western Ontario, 1995–2000. ANOVA included sample size (number of locations per animal season), sex, and individual caribou as fixed effects – none were significant. Least-square means are reported  $\pm$  1 SE

	Movement rate (km/day)	Distance (km)	Sample
Movement rate: ( $F_{4,3949} = 346.7, P = 0.001$ )			
Early winter <sup>a</sup>	a $2.49 \pm 0.059$	$5.41 \pm 0.159$	1301
Late winter	b $0.94 \pm 0.152$	$5.36 \pm 0.415$	192
Spring	c $1.81 \pm 0.065$	$4.56 \pm 0.176$	1071
Calving	d $1.06 \pm 0.086$	$3.05 \pm 0.234$	603
Post-calving	e $1.29 \pm 0.075$	$4.23 \pm 0.205$	787

<sup>a</sup> Tukey multiple range test differences in movement rate for seasons (column) indicated by different letter.



**Fig. 4.** Five seasons of woodland caribou *Rangifer tarandus caribou* that differed relative to: (a) movement rate; (b) seasonal range size; (c) average dispersion; (d) distance moved between seasons. x-axis, mid-point of seasons according to 365 day year with spring starting on day 64 (5 March); error bars,  $\pm$  1 SE.



**Fig. 5.** Distance between successive years for each of the five seasons (spring, calving, post-calving, early winter, late winter) indicating strength of fidelity to seasonal ranges. x-axis, mid-point of seasons according to 365 day year with spring starting on day 64 (5 March); error bars,  $\pm$  1 SE.

winter, which corresponded with the migration seasons of greatest movement rate (Fig. 4b). Smallest range sizes were recorded for calving and post-calving seasons. In contrast to the low movement rate recorded for the late winter season, caribou showed intermediate range size during late winter.

Average dispersion is the average distance between all combinations of locations within a season. The seasonal pattern of dispersion varied among the identified seasons ( $F_{4,277} = 13.15, P = 0.0001$ ) in a different way from the pattern observed for range size and rates of movement. Greatest dispersion occurred during the calving season, whereas lowest dispersion occurred during the subsequent post-calving season (Fig. 4c).

**Seasonal and annual range shifts**

Distance moved between seasons (distance between the centre of a seasonal range) indicated seasonal range shifts ( $F_{4,184} = 3.71, P = 0.0001$ ). Greatest range shifts (> 20 km) occurred from the spring to calving and post-calving to early winter as expected from movement rate results (Fig. 4d). Caribou also shifted range from the early to late winter. In contrast, relatively little change in ranges (< 10 km) occurred from calving to post-calving and late winter to spring. Direct movement from winter (centre of late winter season) to summer (centre of calving season) indicated a  $15.7 \pm 2.2$  km distance for females ( $14.9 \pm 2.2$  for males).

To test seasonal range fidelity, the distance between centre points for each seasonal range was compared from year-to-year. Comparing distances from year-to-year ranges indicated differences among seasons ( $F_{4,40} = 4.74, P = 0.004$ ). Caribou showed relative fidelity to spring, calving, and post-calving ranges, as indicated by distances of < 5 km between seasonal centre points from year-to-year (Fig. 5). In contrast, year-to-year range shifts

of > 10 and 5 km occurred for early and late winter, respectively. Comparing year-to-year ranges indicated that major shifts (> 10 km) in late winter range were common (11 of 18 instances) for female caribou. In contrast, major shifts (> 10 km) in calving range from year-to-year were uncommon and occurred in only two of the 11 comparisons.

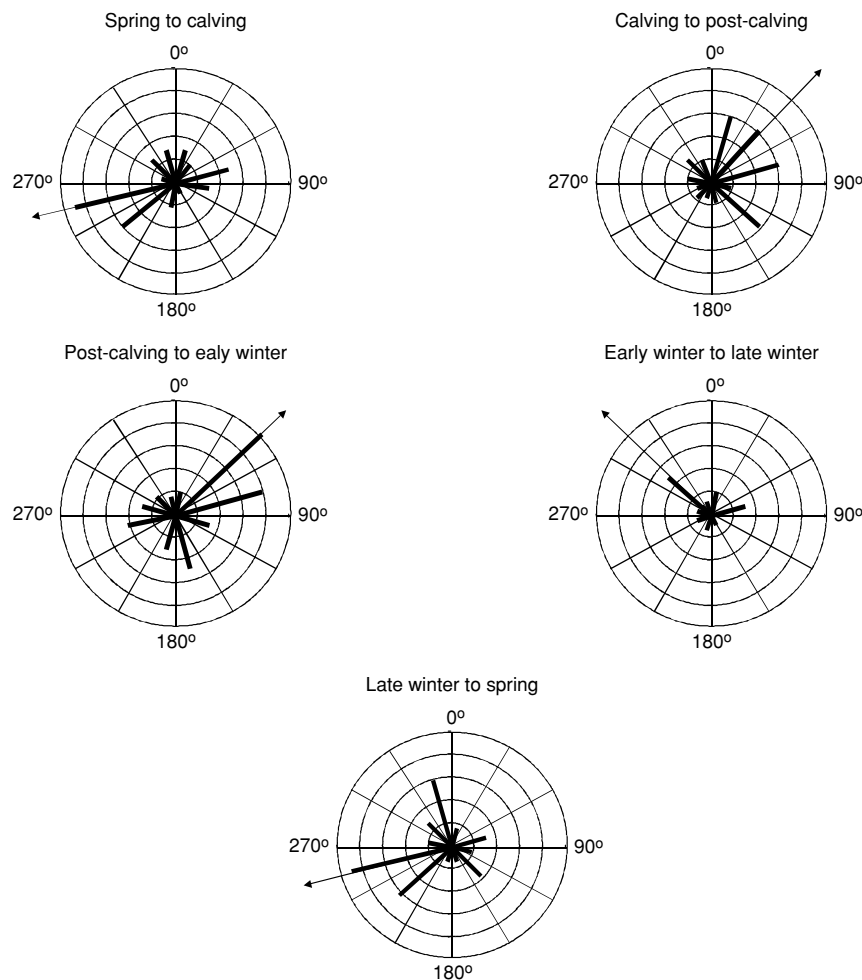
#### Direction of seasonal movements

Direction of movements was generally in an east-west context. From late winter to spring ( $301.4 \pm 81.5^\circ$ ) and spring to calving ( $298.1 \pm 86.4^\circ$ ), caribou generally moved west. In contrast, from calving to post-calving ( $68.2 \pm 69.5^\circ$ ) and post-calving to early winter ( $9.2 \pm 84.2^\circ$ ) caribou generally moved east, although considerable variation occurred among individual caribou. This pattern was corroborated by viewing caribou movements over successive seasons for caribou that were radio-tracked for > 11 seasons (2–4 years; Fig. 6). Most caribou (5 of 11) calved in the west and wintered in

the east, whereas three caribou calved in the east and wintered in the west. Also, two caribou calved in the south and wintered in the north and one caribou calved in the north and wintered in the south.

#### DISCUSSION

Our results indicate the movements of woodland caribou between their summer and winter ranges. Female caribou demonstrated fidelity of calving range that contrasted with variable winter range use. Five seasons best described the seasonal changes in rates of movement for woodland caribou living in north-western Ontario. Greatest rates of movement and largest seasonal ranges were recorded for spring and early winter, seasons identified as periods of migration. The calving season was characterized by low rates of movement, with the exception of the week before assumed parturition when female caribou made relatively swift movements of > 500 m (1.1 km/day). During the calving season, females had the smallest seasonal range while showing the greatest dispersion of locations, which



**Fig. 6.** Direction travelled by woodland caribou *Rangifer tarandus caribou* between five seasons. Thick bars, direction and sample size; each circle represents two caribou; thin line with arrow, median direction.

may relate to a dispersing-out strategy that possibly reduces the risk of predation (Bergerud, 1988). Females showed the greatest fidelity to spring, calving, and post-calving seasons from year-to-year as previously reported for woodland caribou in Labrador (Schaefer, Bergman & Lutich, 2000). In contrast, the location of early and late winter ranges varied considerably from year-to-year. During late winter caribou displayed the lowest rates of movement. Our findings were similar to other woodland caribou research in North America relative to number of seasons, rates of movement, travel seasons, late winter, and calving season (see review Stuart-Smith *et al.*, 1997).

### Delineation of seasons

Previous caribou research has subjectively identified four to six phases based on plant phenology, calving dates, snow cover, and other anecdotal information for woodland caribou living in Saskatchewan (Rettie & Messier, 1998), Alberta (Dyer *et al.*, 2001), British Columbia (Poole, Heard & Mowat, 2000), and Labrador (Bergman, Schaefer & Lutich, 2000). Our methodology incorporated objective (season start and end dates) and partly subjective (number of seasons) decisions to delineate five phases that represented seasonal changes in woodland caribou movements in our study area. Our seasons differed in start and end dates with respect to all previous studies that relied on start of a month (01), midpoint (15) and end of month dates (30 or 31). The British Columbia season dates were the most similar in timing, particularly for summer, early winter, and late winter. However, regional and geographic variations in season dates are expected and analyses need to be specific to a study area.

Improvements on our method would include using additional information in a multivariate analysis to delineate seasonal phases. Additional information intrinsic to the animals that could be used includes activity rates and grouping behaviour, while extrinsic information could include weather patterns and predator movements (e.g. Walton *et al.*, 2001). Also year-to-year variation in seasonal events such as climate conditions would be expected to affect dates for migration and parturition (Stenseth *et al.*, 2002). For example, we speculate that ice conditions that include break-up around 1 May in north-western Ontario and on average freeze-up around 14 November might partially explain seasonal movement patterns (Bergerud, 1996). Additionally, snowfall events have been shown to affect the timing of migration behaviours in caribou (Bergerud, Ferguson *et al.*, 1990; Mahoney & Schaefer, 2002). Lastly, other methods of determining the best model for delineating movements could be investigated (Burnham & Anderson, 2002).

### Rates of movement

Patterns of space use can be described by speed of movement; however caution is necessary with comparisons that use a different time between locations (Ferguson,

Rettie & Messier, 1998). Ignoring possible differences due to time between locations, mean daily distance travelled ranged from 3 to 26 km/day for two barren-ground caribou herds in Alaska-Yukon (Fancy & Whitten, 1991), 14–42 km/day for the George River herd (Bergman *et al.*, 2000), 2–3 km/day for three woodland caribou populations in Labrador (Harrington & Veitch, 1991), 6–11 km/day for the Red Wine Mountain herd (Bergman *et al.*, 2000), to 1 km/day for woodland caribou in Saskatchewan (Rettie & Messier, 2001). For these studies, daily distances of females were lowest during the calving period and highest during spring and autumn when moving between winter and summer range. We observed the same pattern and speculate that low rates of movement by females during the summer relate to a strategy to reduce the opportunities for predation of less mobile neonates.

### Migration seasons

As in our study, more direct movement pathways (Ferguson, Rettie *et al.*, 1998) and greater rates of movement and larger seasonal ranges (Rettie & Messier, 2001) have been reported in autumn. Possibly risk of predation decreases during the autumn breeding season and/or females with calves may switch from reducing predation risk in summer to increasing the opportunity to encounter males during the breeding season (Fuller & Keith, 1981; Rettie & Messier, 2001). Male and female caribou migrated during the same times, although our results do not differentiate possible segregation of seasonal ranges.

In contrast to long-distance migration, which proves effective as coarse-scale anti-predator strategies for migratory caribou, such as barren ground caribou, woodland caribou adopt anti-predator behaviour at the scale of seasonal-range use (Rettie & Messier, 2000). The high degree of range fidelity found during spring and summer (also reported by Rettie & Messier, 2001) indicated that seasonal movements of woodland caribou are different from those of white-tailed deer (Lesage *et al.*, 2000) and moose (Ball, Nordengren & Wallin, 2001). Ferguson, Rettie *et al.* (1998) found greater linearity of female caribou pathways in early spring and autumn suggesting more direct movements to particular habitats. In conclusion, woodland caribou do not make extensive winter–summer migrations but still use a similar range shift to locate seasonal food sources while minimizing predation.

### Late winter season

Trends in movement, group size, and spatial distribution suggest that caribou reduce individual distances and group together during winter (Stuart-Smith *et al.*, 1997). In Saskatchewan during winter, the greater fractal dimension of movements indicated a more tortuous or random movement pathway (Ferguson, Rettie *et al.*, 1998). In other studies, range sizes were larger and rates of movement higher in winter relative to summer (Stuart-Smith *et al.*,

1997; Bergman *et al.*, 2000). In our study, during the late winter season caribou had the lowest rates of movement, seasonal ranges and dispersion were intermediate, and distance travelled from late winter to spring range was short. Previously, the selection by caribou of particular lake size and shape patterns within their winter range (Ferguson & Elkie, in press) was identified, and presumably this requirement differs when lakes are frozen relative to open water seasons. Because caribou shift their range by about 20 km, and the radius of their calving and winter ranges is 5 and 7 km, respectively, our results indicate a low degree of summer and winter overlap.

### Calving season

Movements and spatial distribution of woodland caribou suggest that individual female caribou may be spreading out or distancing themselves from other parturient females during summer (Fuller & Keith, 1981; Stuart-Smith *et al.*, 1997; Rettie & Messier, 2001). Individual females may be spacing-out from each other to reduce the risk of predator encounters during calving and post-calving while the calf is less mobile and more susceptible to predation (Bergerud, Ferguson *et al.*, 1990). Locations of females were found to be greatly dispersed during the calving season and females also had a decreased movement rate and a small range size during calving and post-calving seasons.

A mean calving date of 1 June was suggested by an increase and then subsequent decrease in movement rate. The mean parturition date was indicated by a spike in movement rate that represented a long-distance movement during the week before the peak (1 June) followed by a brief (3 day) sedentary period of low movement rate. A similar spike in movement rate was observed in May for Red Wine caribou (Bergman *et al.*, 2000). Bergerud (1996) suggested that it might be advantageous for sedentary caribou to disperse and arrive at a chosen calving site just before parturition. Additionally, radio-tracking data of moose in north-western Ontario also found a movement just before parturition which may be a strategy to lose predators (Welch, 2000). Backdating from calving date using a gestation length of 229 days (Bergerud, 1975) suggests a peak rut date of 15 October. Thus, demarcating changes in rates of movement has applicability in determining life-history events using telemetry location data.

For caribou, range fidelity has been described for the calving period (Gunn & Miller, 1986; Fancy & Whitten, 1991; Schaefer, Bergman *et al.*, 2000). For migratory caribou, fidelity to traditional calving grounds has been considered stronger than fidelity to other seasonal ranges (Gunn & Miller, 1986). In contrast, woodland caribou are more sedentary and exhibit over-dispersion around the time of parturition (Bergerud, Ferguson *et al.*, 1990). Schaefer, Bergman *et al.*'s (2000) results indicated that parturition represents only the initiation of fidelity, which is continued through the autumn breeding season for

both migratory and sedentary caribou. Our results also indicated little movement between calving and post-calving; however, a shift to winter range was found during the autumn period. Relative to males, female caribou may have decreased rates of movement during the calving and post-calving periods as suggested by Fig. 2. However, this difference was not statistically significant, perhaps owing to the limited number of males sampled. Interestingly, no increase in movement rate was observed during the July–August fly season as observed in other caribou populations (Hagemoen & Reimers, 2002).

### Management implications

Large mobile animals, such as caribou, are most vulnerable to anthropogenic disturbance because of their need for large spaces (Harestad & Bunnell, 1979; Schaefer, Veitch *et al.*, 2001). In Ontario, forest management guidelines have been designed for the long-term maintenance of caribou populations (Racey *et al.*, 1999); however, it is not clear yet what logging strategies will meet the spatial and foraging needs of caribou (Smith *et al.*, 2000). Our findings, like other studies, suggest that the strongest seasonal fidelity is to calving areas. We do not argue that calving areas are necessarily the most important habitat for woodland caribou. However, we do suggest that weaker fidelity for the winter seasons and stronger fidelity for calving indicate that woodland caribou are more flexible in choosing winter areas or that the attributes required for their winter range, such as food availability, predator avoidance, and perception of security, change from year-to-year. For seasonal migrations, both males and females changed ranges in relative synchrony, although our data on males were limited. As a result, we recommend that male and female caribou be managed similarly relative to the need for specific travel corridor requirements. In contrast, specific management requirements may be necessary for conservation of woodland calving habitat for parturient females which likely differ between males and females. Further research is required to identify the fine large-scale habitat attributes of preferred calving and winter areas that include use of lakes and wetland complexes and terrestrial forest types.

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