

Using movement behaviour to define biological seasons for woodland caribou

Tyler D. Rudolph & Pierre Drapeau

Centre for Forest Research, Department of Biological Sciences, Université du Québec à Montréal, NSERC Industrial Chair in Sustainable Forest Management C.P. 8888, succursale Centre-ville, Montréal, QC, Canada, H3C 3P8. Corresponding author: tylerdrudolph@gmail.com

Abstract: Terrestrial mammals are strongly influenced by seasonal changes in environmental conditions. Studies of animal space use behaviour are therefore inherently seasonal in nature. We propose an individual-based quantitative method for identifying seasonal shifts in caribou movement behaviour and we demonstrate its use in determining the onset of the winter, spring dispersal, and calving seasons. Using pooled data for the population we demonstrate an alternate approach using polynomial regression with mixed effects. We then compare individual onset dates with population-based estimates and those adopted by expert consensus for our study area. Distributions of individual-based onset dates were normally distributed with prominent modes; however, there was considerable variation in individual onset times. Population-based estimates were closer to the peaks of individual estimates than were expert-based estimates, which fell outside the one-tailed 90% and 95% sample quantiles of individually-fitted distributions for spring and winter, respectively. Both expert- and population-based estimates were later for winter and earlier for both spring and calving than were individual-based estimates. We discuss the potential consequences of neglecting to corroborate conventionally used dates with observed seasonal trends in movement behaviour. In closing, we recommend researchers adopt an individual-based quantitative approach and a variable temporal window for data set extraction.

Key words: biological inference; quantitative methods; seasonal onset behaviour; temporal variation; woodland caribou.

Rangifer, Special Issue No. 20: 299–311

Introduction

The life history traits of mammals are in no small part a function of the bioclimatic environments in which they live (Klein, 1982). In the northern boreal forest of Canada, the biological activity of terrestrial mammals is regulated by seasonal shifts in temperature and precipitation which, in turn, directly or indirectly influence the quality and availability of forage and refuge habitat (Pruitt, 1957; Telfer & Kelsall, 1984; Post & Stenseth, 1999). Members of the Cervidae family, for example, exhibit growth dormancy in winter when the metabolic demands of thermoregulation are high and plant nutrients essential for body tissue development are in short supply

(Irving *et al.*, 1955; Wood *et al.*, 1962; McEwan, 1970). Likewise, displacements are limited at this time in order to minimize heat loss and the depletion of body reserves (McEwan & Whitehead, 1970; Ozoga & Gysel, 1972; Gates, 1979; Ferguson & Elkie, 2004). Spring, in contrast, is a time of increased energetic expenditure when the demands of pregnancy reach their peak and female cervids prepare to give birth (Moen, 1976). Forest-dwelling woodland caribou (*Rangifer tarandus caribou*) make concerted movements away from wintering areas at this time as a means of attaining low densities and thereby reducing detection by predators (Bergerud & Page, 1987; Cumming & Beange, 1987; Rudolph, 2011). The

punctuated movements of spring dispersal come to an abrupt halt at parturition, when nursing caribou become virtually immobile, functionally limited in their movements for up to several weeks until calves are vigorous enough to travel (Lent, 1966; Espmark, 1971; Clutton-Brock & Guinness, 1975). This period coincides with the emergence of high-quality plant vegetation required for lactation and, consequently, calf development (Klein, 1990; Lantin *et al.*, 2003; Post *et al.*, 2003).

Like many species, caribou exhibit shifts in biological activity that parallel changes in their natural environment. For this reason, investigations of their space use behaviour tend to differentiate between seasons based on conventional knowledge of populations, climatic conditions, and plant phenology (e.g. Rettie & Messier, 2000; Brown *et al.*, 2003, Apps *et al.*, 2001; Jones *et al.*, 2007; Hins *et al.*, 2009). Few studies, however, recognize and account for temporal variation in seasonal processes, which could have important consequences for biological inference. Calving, for example, is a relatively predictable biological event that tends to be well defined for populations based on field observations (Rettie & Messier, 2001). Despite this, the peak onset of calving can vary annually by as much as 15 days (Eloranta & Nieminen, 1986; Cameron *et al.*, 1993; Post & Klein, 1999; Flydal & Reimers, 2002). Furthermore, calving times for individuals within a population may vary by as much as a month or more (Bergerud, 1975; Eloranta & Nieminen, 1986; Rettie & Messier, 1998; Post & Klein, 1999; Ferguson & Elkie, 2004). Conceivably, then, failure to account for either source of variation (whether individual or annual) could mean including several weeks of migratory behaviour in a characterization of caribou calving site selection.

However accurate the dates we choose, using a fixed temporal window to study seasonal phenomena may generate biased results due to inter-individual variation. Given the variable and often unpredictable behaviour of free-ranging animals (Gustafson & Gardner, 1996; Johnson *et al.*, 2001; Gustine, 2005), we propose an approach to analyzing seasonal space use that accounts for individual variation in seasonal onset times. We argue that by varying the temporal window of analysis to more effectively capture the biological phenomenon under investigation, we can improve ecological studies by reducing misclassification, thereby improving biological inferences.

A number of quantitative approaches have been used to identify seasonal shifts in the behaviour of woodland caribou. These require *a priori* biological knowledge and can be rule-based (Mahoney & Schaefer, 2002; Saher & Schmiegelow, 2005; Courbin

et al., 2009) or model-based (Ferguson & Elkie, 2004; Dyke, 2008; Vander Wal & Rodgers, 2009). We propose a model-based approach called recursive partitioning, which can be used to locate changes in the distribution of movement parameters over time using iterative analyses of variance (ANOVA) and prior knowledge of species life history. We demonstrate how this approach can be used to delineate three contrasting seasonal periods in the annual life cycle of woodland caribou: winter, spring dispersal, and calving. Finally, we compare the results of this approach with 1) dates obtained using polynomial regression with pooled data (population estimates), and 2) dates adopted by expert consensus (conventional estimates) for our study area in northern Quebec.

Study area

The study area comprises a 109,116 km² tract of boreal forest in northern Quebec situated between 49°52' and 51°46'N and 71°17' and 79°31'W (Fig. 1). Part of the black spruce-feathermoss bioclimatic domain, it is dominated by black spruce (*Picea mariana*) in association with feathermoss (*Pleurozium schreberi*) and/or various lichen species. Jack pine (*Pinus banksiana*) and balsam fir (*Abies balsamea*) occur to a lesser extent, in addition to trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), tamarack (*Larix laricina*), and (rarely) balsam poplar (*Populus balsamifera*). Forest understory is dominated by mosses and ericaceous shrubs with few herbaceous species. The western flank of the region forms part of the Clay Belt and is dominated by large sphagnum bog and fen complexes. Terrain is broad and mildly sloping with occasional topographic relief. Elevation ranges from 45 to 825m and there are numerous rivers and waterways interconnecting the region. Treed wetlands and upland forest intersperse with bog/fen complexes and lichen or shrub-dominated uplands with occasional rock barrens. The region receives approximately 960 mm of precipitation annually with monthly average temperatures ranging from -19° (January) to + 16° (July) Celsius.

Constituting Québec's second-largest timber supply region, the study area encompasses both the northern limit of commercial forestry activity and the southern limit of continuous woodland caribou distribution (Courtois, 2003). Primary disturbances include forest fire (100-500 year fire cycle; Bergeron *et al.* 2001) and forest harvesting, which is presently concentrated in the southern portion of the study area. Large mammal species in addition to forest-dwelling woodland caribou include, moose (*Alces alces*), wolf (*Canis lupus*) and black bear (*Ursus americanus*). Reliable population estimates are unavailable,

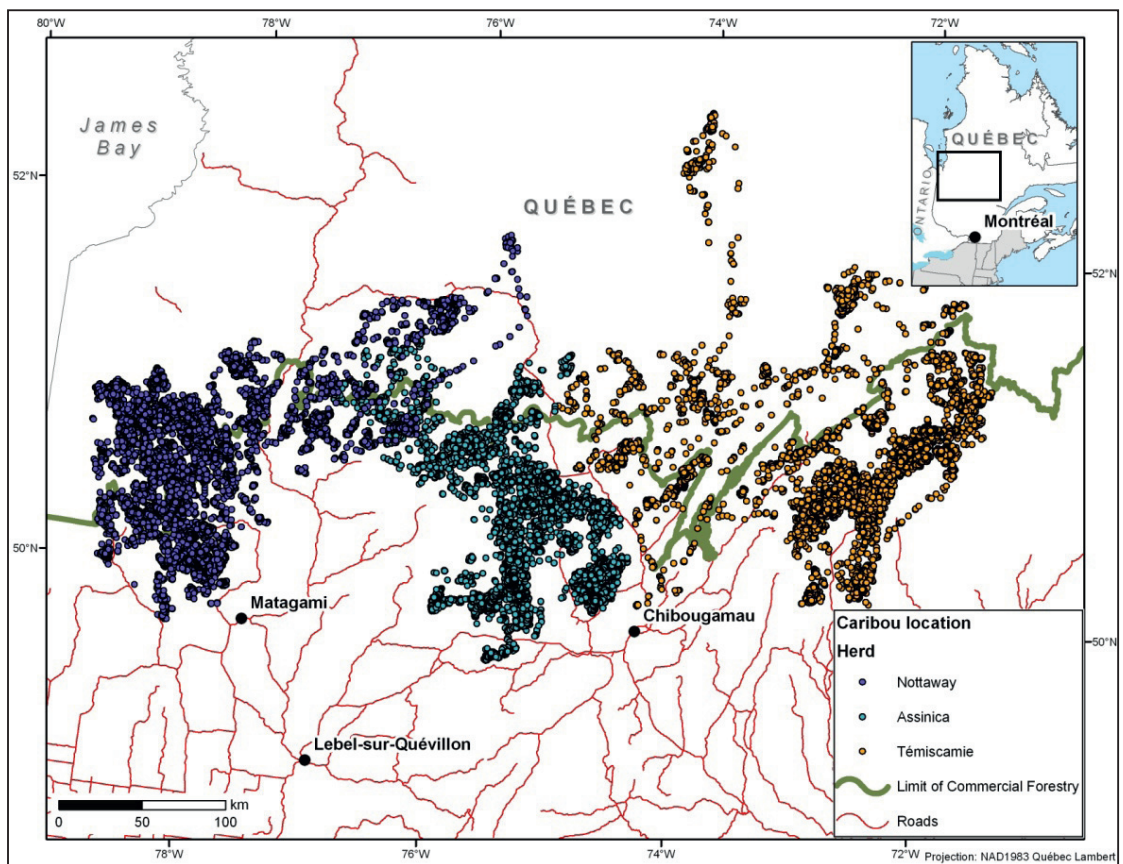


Fig. 1. Location of study area in the northern boreal forest of Quebec. Depicted are GPS telemetry locations transmitted by 26 collared female woodland caribou dispersed across three regional populations: the Nottaway, Assinica, and Témiscamie. Primary road networks are also depicted along with the current limit of commercial forestry.

but caribou densities are estimated to be between 1.5 and 2.1/100 km², with individuals occupying average annual home ranges of ~4386 km² (St-Pierre *et al.*, 2006). In the northern sector, infrequent range overlap takes place with populations of the tundra-forest ecotype of woodland caribou (*Rangifer tarandus caribou*) (Courtois *et al.*, 2003).

Methods

Caribou capture and GPS telemetry

Animal relocation data were obtained via GPS (Global Positioning System) collar transmitters (Telonics model TGW 3680) fitted on 26 female caribou by members of the Québec Ministry of Natural Resources and Wildlife in March 2004 and January 2005. Captures were conducted using ASTAR 350BA or EC120 helicopters and a net gun (Potvin & Breton, 1988). Individuals sampled were evenly distributed across three regional populations: the Nottaway (west), Assinica (central), and Témiscamie

(east) (Fig. 1). Collars were programmed to transmit locations every seven hours and data was compiled in March 2007. Relocations were filtered for positional accuracy in order to remove large location errors: those based on 4 or more satellites (3-D) were eliminated if they had corresponding horizontal dilution of precision (HDOP) values greater than or equal to 25, whereas those based on 3 satellites (2-D) were eliminated if they had HDOP values greater than or equal to 8 (Dussault *et al.*, 2001). The Horizontal Dilution of Precision reflects the horizontal accuracy (latitude/longitude) of GPS position fixes by adjusting the error estimates according to the geometry of the satellites used. This resulted in a roughly 4% data reduction per individual.

Although movement rates have been known to vary among female caribou according to reproductive status (Paré & Huot, 1985; Fancy & Whitten, 1991; Ferguson *et al.*, 1998), high pregnancy rates are pervasive in woodland caribou populations so we assumed

no error due to variation in reproductive condition (Parker, 1981; Rettie & Messier, 1998).

In order to render our data temporally uniform, we reduced data sets to one relocation per individual per day, retaining that relocation obtained closest to 12:00 noon. Because estimates of movement rates may be biased when fix interval varies (Johnson *et al.*, 2002), distance calculations based on more than one consecutive day between successive relocations were not retained for analyses. Furthermore, individual-year combinations comprising less than 100 observations were eliminated from analyses. Resulting sample sizes ranged from 231 to 365 (\bar{X} = 319).

Temporal focus of study

We chose the winter, spring and calving seasons because they represent critical periods in the annual life cycle of woodland caribou (Darby & Pruitt, 1984; Environment Canada, 2008). We were also particularly interested in characterizing spring dispersal behaviour of boreal caribou (Rudolph, 2011). Our goal, therefore, was to identify peak onset dates for the winter, spring dispersal, and calving periods on an individual basis through quantitative analysis of movement patterns. We began by calculating two movement parameters for each individual: movement rate (km/day) and net displacement (km). Movement rate was logarithmically transformed to improve normality. Net displacement was defined as the Euclidean distance between an animal's location on any given day and its location on January 10 of the same year; this date was chosen as the "anchor" point because most individuals were found to have settled into their wintering areas by this time. We then proceeded to calculate daily averages for each parameter (individuals and years pooled). Visualizing trends in pooled averages over time permitted us to identify temporal neighbourhoods corresponding with seasonal changes in the movement behaviour of our study population. All computations were done using R Version 2.9.0 (R Development Core Team 2010) (R code is available through the authors upon request).

Individual-based modeling

In order to minimize noise attributed to periodic variation in individual movement behaviour (e.g. circadian rhythms), prior to proceeding we applied a 4-term (1 observation/day) smoothing window (moving average) over the raw movement parameters observed for each individual-year time-series (Rudolph, 2011). We chose 4 terms because correlograms of residual distances (y) over time (x) demonstrated a significant recurring pattern every 4 days

for the majority of individual-year distributions based on Moran's *I*.

We used the R package *rpart* to model movement rate (km/day) and net displacement (km) as a function of Julian day (origin = January 1) using recursive partitioning to progressively subdivide the smoothed values into temporally homogenous groups (De'ath & Fabricius, 2000; Therneau *et al.*, 2010). Smoothed movement rates were log-transformed to improve normality. The *rpart* algorithm iteratively performs analyses of variance to produce a univariate regression tree in which temporally discrete blocks are optimally partitioned so as to maximize the between-groups sums of squares (Therneau & Atkinson, 2011). A complexity parameter is incorporated to permit only those partitions which improve the explained variance by an established threshold (i.e. $\Delta R^2 \geq 0.01$). Cross-validation is employed to obtain the predicted error, and the optimal tree is determined based on the lowest estimate plus or minus one standard error.

In order to determine individual onset dates for winter, spring dispersal and calving, we conducted two recursive partitioning exercises (one for each parameter or response variable) for each individual-year distribution. Due to inherent variation in movement behaviour, there were occasionally numerous statistically plausible choices for the onset of a given season, which necessitated *a priori* knowledge of caribou biology. The first model ($\log(\text{movement rate}) \sim \text{Julian day}$) provided the candidate breakpoints. Since spring dispersal is generally demarcated by important displacements from late winter ranges to traditional calving areas (Courbin *et al.*, 2009), breakpoints obtained via the second model ($\text{net displacement} \sim \text{Julian day}$) gave weight to our final choice of onset dates, in particular with respect to the beginning and end of spring dispersal (Fig. 2).

In order to provide enough data to effectively capture the onset of winter, we included the previous year in recursive partitioning exercises when selecting for these dates. Individuals displaying erratic behaviour (i.e. considerable deviation from mean observed pattern) and those missing data during critical periods of interest were excluded from subsequent analyses for the year(s) in question. Once the onset dates of winter, spring dispersal, and calving had been determined for every qualifying individual-year data sequence, population means (μ) and their associated standard errors (SE) were estimated for each season using a non-parametric bootstrap procedure (Efron & Tibshirani, 1986). Means were considered the most appropriate summary statistic given that individual onset dates were normally distributed.

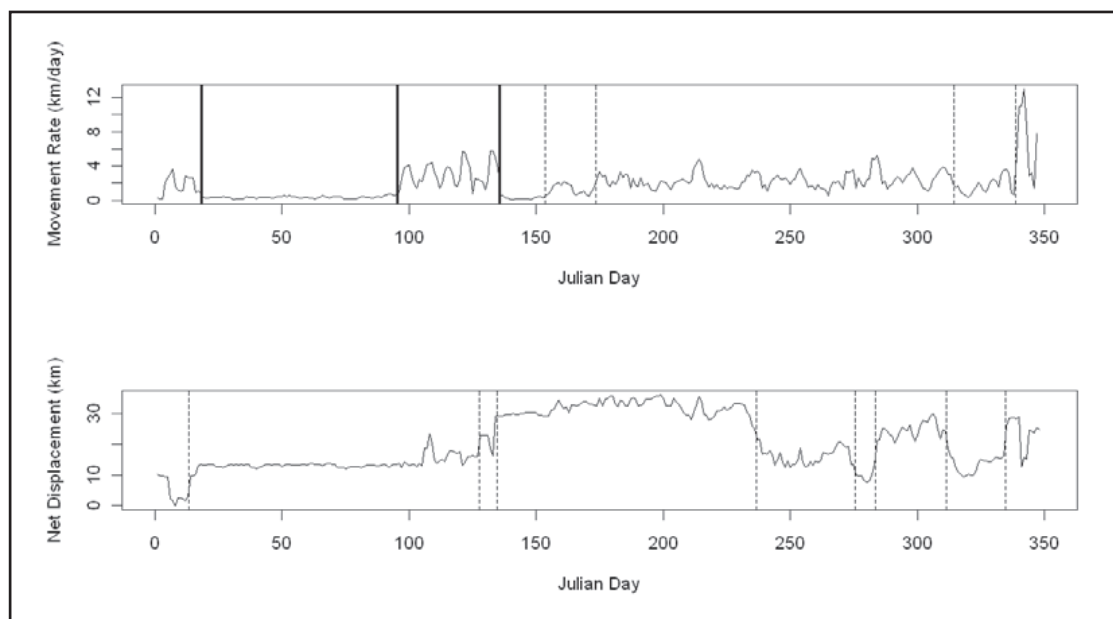


Fig. 2. Example output from two recursive partitioning exercises conducted using GPS telemetry locations emitted daily by one female caribou of Northern Quebec in 2005. Model 1 (log(distance)~Julian day) is depicted above and Model 2 (net displacement~Julian day) is depicted below. Dashed lines represent candidate splits of the univariate regression trees and solid black lines represent splits chosen to delimit the onset of (from left, above) winter, spring dispersal, and calving. Because important changes in net displacement may be indicative of spring dispersal, breakpoints obtained via Model 2 (below) informed our choice of final onset dates when more than one candidate split was obtained by Model 1 for a given season.

Population-based modeling

As a point of comparison, we developed a population-based polynomial regression model with mixed effects in order to estimate the onset dates of winter, spring dispersal, and calving periods based on season-specific shifts in movement rate (log-transformed to improve normality) as a function of Julian day (origin = Jan. 01). This is similar to the approach published by Ferguson & Elkie (2004); however because we were working with a sample of a much larger population and wished to take into account individual and annual variability in seasonal onset behaviour, a random intercept was specified for each individual and each nested individual-year combination. Specifying the grouped structure of the data ensured that the individual animal was considered the sample unit and that population estimates were unaffected by variable sample sizes (Gillies *et al.*, 2006). Population-based models were estimated using Maximum Likelihood and the R package nlme (Pinheiro *et al.*, 2010). Polynomials were independently re-centered about their respective means (orthogonal polynomials) to facilitate convergence and eliminate correlation between terms. The model takes the following form:

$$y_i = X_i\beta + Z_i b_i + \epsilon_i, \text{ where:}$$

$X_i\beta = \beta_0 + \beta x + \beta x^2 + \beta x^3 + \dots + \beta x^k$ is the standard linear model structure for the fixed effects component, and:

$Z_i b_i = b_1 x + b_2 x^2 + b_3 x^3 + \dots + b_k x^k$, where b_k is the variance-covariance matrix of the random effects and ϵ_i is an estimation of the residual error.

We compared a series of candidate models in which polynomial terms were sequentially added and Akaike's Information Criterion for small sample sizes (AIC_c) was calculated iteratively to identify the best candidate model based on the principle of parsimony. In order to define at least three seasons, we began with five terms and sequentially added up to 25 polynomial terms, stopping at the first model in the sequence where ΔAIC_c ceased to be negative, the best candidate model being the one immediately prior. Inflection points in the fitted curve indicated season-specific changes in movement rate, and these were obtained by solving for $x=0$ in the second derivative of the fixed effects component of the regression equation (Ferguson & Elkie, 2004).

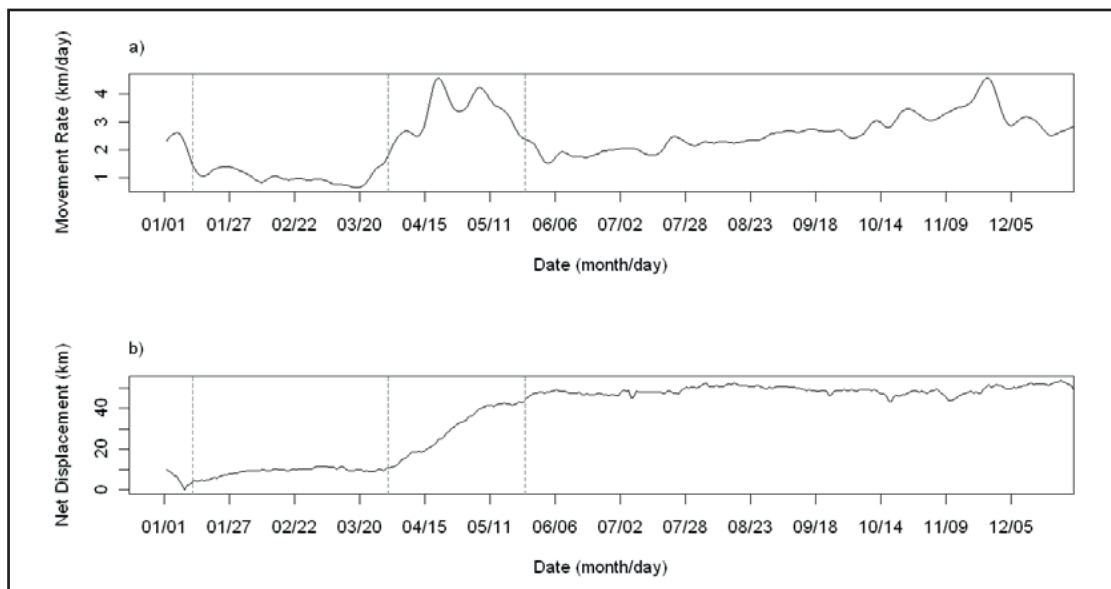


Fig. 3. Mean daily a) movement rate (smoothed) and b) net displacement of 26 female woodland caribou from Northern Quebec pooled across 3 years (2004–2007). Movement parameters (1 observation/day per individual) were derived from GPS locations transmitted from ARGOS telemetry collars. The onset of late winter is marked by a significant drop in movement rate in early January (1st dashed line from left). The onset of spring dispersion is marked by a sudden increase in both movement rate and net displacement in early April, followed by a drop in both variables in late May that marks the onset of calving (rightmost pair of dashed lines).

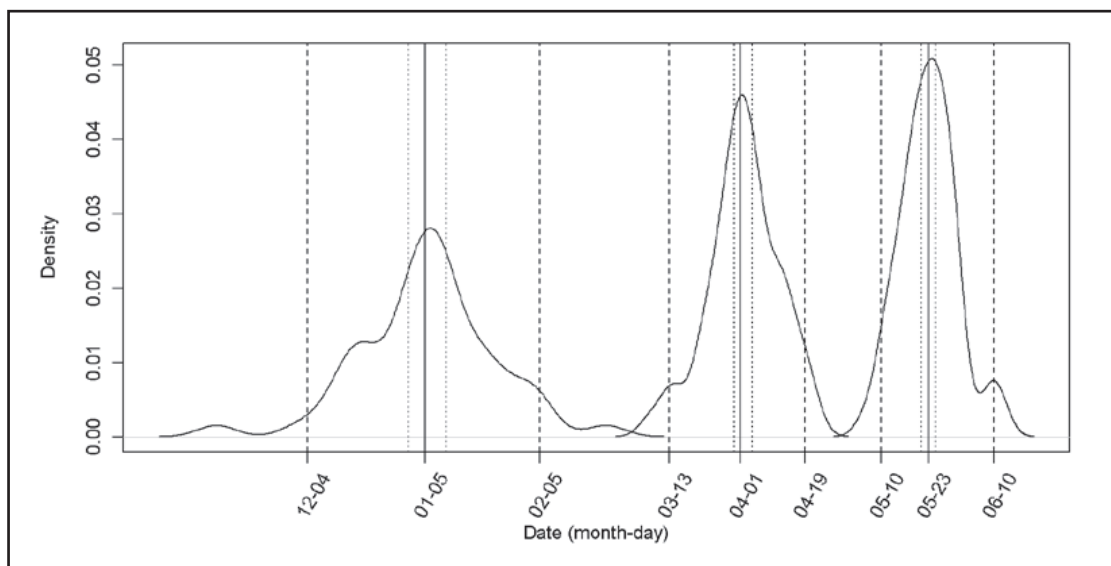


Fig. 4. Distribution of individual onset dates determined via recursive partitioning for 26 female caribou from Northern Quebec pooled over three years. Movement rate (km/day) and net displacement (km) were derived from GPS locations transmitted from ARGOS telemetry collars. The two parameters were subsequently modeled as a function of time using iterative analyses of variance (ANOVA). Onset dates for all three seasons were normally distributed with prominent modes. Solid lines indicate peak (population) onset dates for the winter (Jan. 5; $n=50$), spring dispersal (April 1; $n=55$), and calving (May 23; $n=62$) periods. Dotted lines indicate the 95% confidence intervals about the means (peak onset dates) and dashed lines indicate the 95% sample confidence intervals.

Table 1. Peak annual onset dates for the winter, spring dispersal, and calving seasons as determined by individual-based recursive partitioning (2004-2007). Also shown are sample sizes (n = number of collared caribou from which onset dates were derived), 95% bootstrap confidence intervals (Lower CI, Upper CI), standard errors about the mean estimates, and overall season length. An estimate of season length for winter 2007 was not possible as no GPS locations were recorded beyond March 2007.

Year	Season	n	Lower CI	Peak Onset	Upper CI	S.E. (days)	Length (days)
2005	winter	13	9-Jan	17-Jan	27-Jan	4.5	74.8
2006	winter	21	30-Dec	5-Jan	11-Jan	3.4	81.2
2007	winter	16	19-Dec	28-Dec	6-Jan	4.4	n/a
2004	spring	12	6-Apr	11-Apr	15-Apr	2.3	44.5
2005	spring	22	31-Mar	2-Apr	5-Apr	1.4	50.0
2006	spring	21	24-Mar	28-Mar	2-Apr	2.3	55.1
2004	calving	18	22-May	25-May	29-May	1.7	15.0
2005	calving	25	20-May	23-May	26-May	1.6	20.4
2006	calving	19	18-May	21-May	25-May	1.6	25.8

Results

Average distances travelled per day (pooled for all individuals and years) are shown in Fig. 3a. Corresponding with the onset of late winter, a significant drop in movement rate was noted to take place in early January. A sudden increase in movement rate in early April corresponded with the onset of spring dispersal, followed by a substantial drop in movement rate which indicated the start of calving in late May. Between January 10 and June 30, the minimum daily average distance was 530 m on March 16 while the maximum daily average distance was 5.93 km on April 21. The maximum distance recorded in one day was 54.6 km by caribou 2003014 on May 9.

Average net displacement per day (pooled for all individuals and years) is depicted in Fig. 3b, which reveals a distinct migratory pattern from early April until late May. On average there was little departure from wintering areas until the onset of spring dispersal, at which time animals proceeded to travel consistently further away from their wintering areas, reaching a maximum daily average displacement of 49.3 km from their wintering grounds on June 6. The maximum net displacement recorded for one animal between January 10 and June 15 was 208.8 km by caribou 2003008 on June 09, 2005.

Individual-based models

The distributions of seasonal onset dates determined via individual-based recursive partitioning are shown in Fig. 4. Peak onset of late winter occurred on Janu-

ary 5th (+/- 5.2 days, $n = 50$, $s = 18.64$), spring dispersal on April 1nd

(+/- 2.5 days, $n = 55$, $s = 9.73$), and calving on May 23th (+/- 2.0 days, $n = 62$, $s = 7.78$). Distributions exhibited prominent modes in all three cases, and Anderson-Darling tests of residual values ($f(x) = x - \bar{x}$) indicated no significant departure from normality. Sample 95% confidence intervals ranged from Dec. 04 – February 05 for winter, March 13 – April 19 for spring dispersal, and May 10 – June 10 for calving. Peak onset times over three years varied from Dec. 28 (2007) to Jan. 17 (2005) for winter (20 days), from March 28 (2006) to April 02 (2005) for spring (5 days), and from May 21 (2006) to May 25 (2004) for calving (4 days) (Table 1).

Winter was the longest season at $\mu = 78.6$ days, followed by spring dispersal at $\mu = 50.6$ days, and finally calving at $\mu = 20.2$ days. Based on the statistics of unique individuals, the longest period observed for winter behaviour was 130 days, for spring dispersal behaviour 80 days, and for calving behaviour 58 days. Minima and maxima were Nov. 9 and February 24 for winter (107 days), March 8 and April 22 for spring dispersal (45 days), and May 6 and June 13 for calving (38 days).

The onset of late winter (2005 vs. 2007: $F = 9.70$, $P < 0.01$) and spring dispersal (2004 vs. 2006: $F = 15.0$, $P < 0.001$) tended to be progressively earlier from 2004 to 2007. This may have been attributed to higher early snowfall (for winter) and/or higher March temperatures (for spring) in latter years. Latitude had no significant influence on onset dates regardless of season. Lastly,

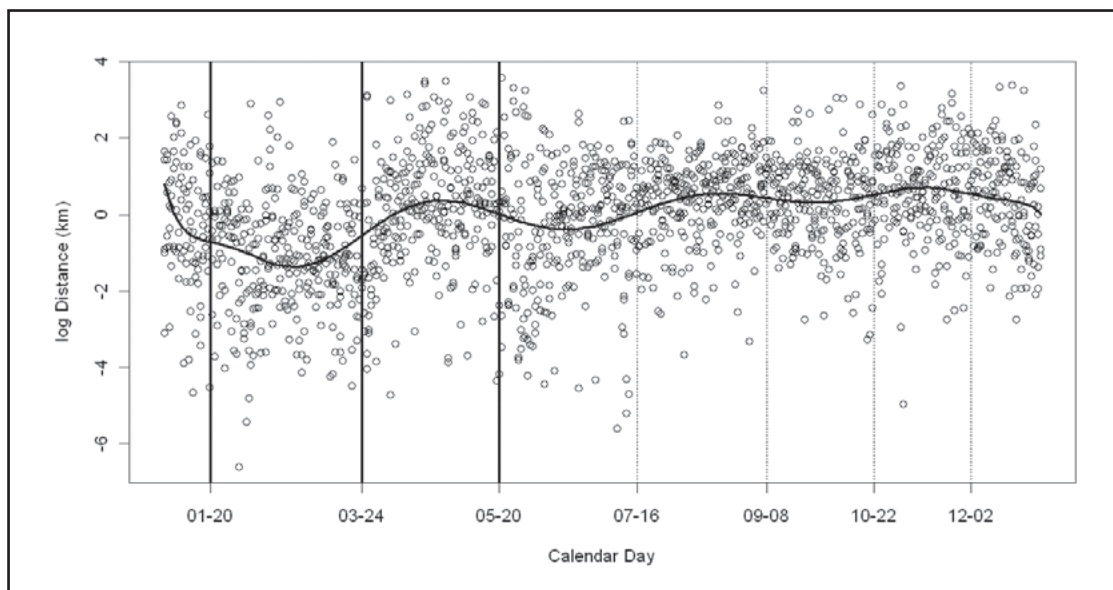


Fig. 5. Distance (in km, log-transformed) travelled per day over time by 26 woodland caribou tracked using GPS telemetry in Northern Quebec. Shown are raw values and the fitted curve of an 11th order polynomial regression model. Inflection points were obtained by solving for $x=0$ in the second derivative of the fixed effects component of the regression equation. Solid lines indicate the estimated peak onset of the winter (January 10), spring dispersion (March 24), and calving (May 20) periods, while dotted lines indicate latter seasons of potential biological interest (most likely representing summer, fall, rut, and early winter).

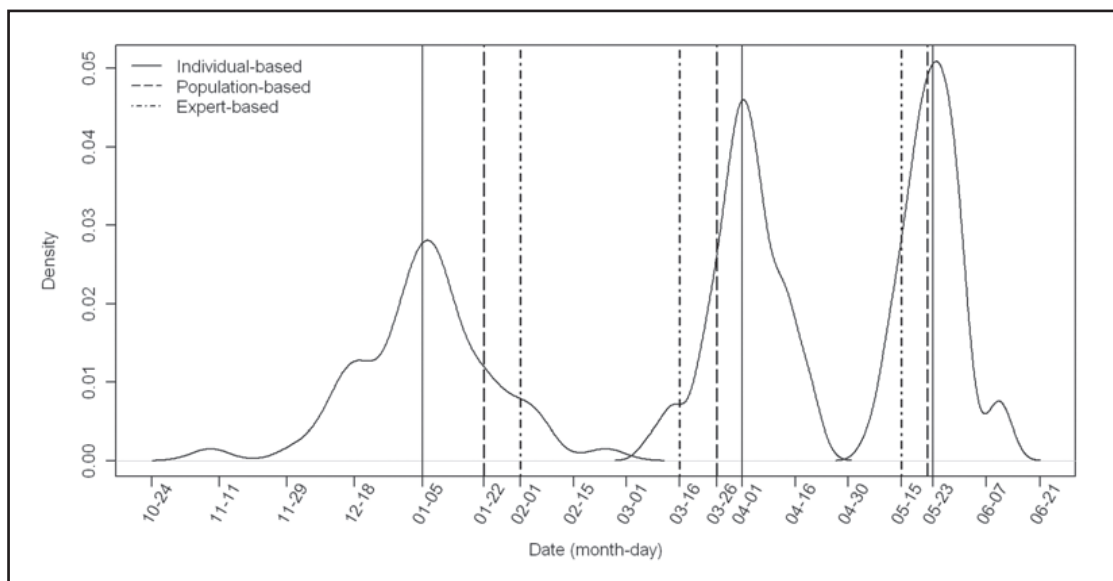


Fig. 6. Comparison of peak onset dates corresponding with (from left to right) the winter, spring dispersal, and calving periods. Dates were obtained using three methods: a) individual-based recursive partitioning (solid lines), b) mixed polynomial regression with pooled data (dashed lines) and c) expert consensus (dot-dashed lines). Conventional estimates for spring and winter were outside the respective one-tailed 90% and 95% sample quantiles of the individually-fitted distributions. Analyses were conducted using movement parameters derived from GPS telemetry locations of 26 female woodland caribou in Northern Quebec.

although age and experience can influence the timing of ovulation and therefore calving (Bergerud, 1975; Flydal & Reimers, 2002; Langvatn *et al.*, 2004), morphometric data available for our population was not complete enough to support or refute this.

Population-based model

Adding progressive polynomial terms to the prospective regression model continued to substantially reduce AIC_c until a twelfth term was added, at which time the net change in AIC_c became positive. Therefore the final population-based model contained eleven polynomial terms and took the following form (jd = Julian day):

$$\hat{Y} = 1.08 - 0.301 + 2.16 \times 10^{-2} (\text{jd})^2 - 8.18 \times 10^{-4} (\text{jd})^3 + 1.71 \times 10^{-5} (\text{jd})^4 - 2.11 \times 10^{-7} (\text{jd})^5 + 1.63 \times 10^{-9} (\text{jd})^6 - 7.97 \times 10^{-12} (\text{jd})^7 + 2.51 \times 10^{-14} (\text{jd})^8 - 4.92 \times 10^{-17} (\text{jd})^9 + 5.44 \times 10^{-20} (\text{jd})^{10} - 2.60 \times 10^{-23} (\text{jd})^{11} + \text{Zibi} + \epsilon_i$$

Relative to the fixed intercept, there was considerable variation in the random intercepts for “id” and “year within id” (16.6% and 18.1%, respectively). Solving for x=0 in the second derivative of the fixed effects component of the regression equation allowed us to determine the estimated peak onset dates of the three biological seasons of interest for our study population: late winter (January 20), spring dispersal (March 24) and calving (May 20) (Fig. 5).

Comparison of Methods

With respect to quantitative methods (individual- vs. population-based), estimates of winter were 16.6 days apart ($p = 0.20$), with the pooled estimate occurring later (Fig. 6). Estimates of spring dispersal were 7 days apart ($p = 0.21$), with the individual-based estimate occurring later. The least difference occurred among estimates of peak onset for calving, with the pooled estimate preceding the individual-based estimate by only 1.6 days.

Estimates of peak winter onset differed greatly between individual- and expert-based (conventional) approaches, with the conventionally defined period occurring close to a full month (26.6 days) later than it was found to occur by recursive partitioning (Fig. 6). Conventional estimates for the onset of spring dispersal, likewise, preceded the observed mean date by over two weeks (16.9 days). Again the least amount of difference between estimates was observed for peak calving time, with conventional dates preceding individual-based results by just over a week (8.6 days). The conventional estimate for winter was outside the one-tailed 90% sample quantiles of the individually-fitted distribution; the estimate for spring was outside the one-tailed 95% sample quantiles.

Discussion

By delineating seasonal shifts in movement behaviour using individual-based recursive partitioning, we were able to capture both individual and annual variation in the seasonal onset behaviour of woodland caribou. In terms of individual variation, the onset of calving alone spanned up to 38 days in length from the earliest recorded observation (May 6) to the last (June 13). In terms of annual variation, over three years peak onset varied by up to 20 days for winter, although only 4–5 days for spring and calving. These findings, particularly with respect to calving, corroborate with what has been documented elsewhere for woodland caribou (Bergerud, 1975; Rettie & Messier, 1998; Ferguson & Elkie, 2004), barren-ground caribou (Cameron *et al.*, 1993; Post & Klein, 1999), and Eurasian reindeer (Eloranta & Nieminen, 1986; Flydal & Reimers, 2002).

Despite the fact that individually-estimated onset dates were normally distributed with prominent modes for all three seasons, consensus-based estimates of peak onset dates were outside the one-tailed 90% and 95% confidence intervals observed for winter and spring, respectively. This suggests that researchers should use caution when adopting conventionally accepted seasonal periods in biological investigations of seasonal phenomena. As shown by our example, a quantitative approach using pooled data rendered considerably more accurate estimates of peak shifts in seasonal behaviour. In fact, if we had used recursive partitioning on the pooled data instead of polynomial regression, we would have obtained peak estimates roughly identical to the mean values reported from individual-based estimates (Rudolph & Drapeau, unpubl. data).

Seasonal changes in movement rates have been documented for a great number of species (Moen, 1978; Jingfors, 1982; Garner *et al.*, 1990; Covell *et al.*, 1996; Schneider *et al.*, 2000; Brito, 2003). By modeling these changes we can derive inflection points marking the boundaries between statistically distinct periods of biological interest. This is typically achieved through some form of non-linear curve-fitting, and may be applied to individual (individual-based) or pooled (population-based) distributions. Vander Wal & Rogers (2009), for example, approximated the cumulative annual distance travelled by individual moose with a sigmoidal relationship. Movement rates of woodland caribou, however, tend to be fairly irregular over time, and such trends can be difficult to approximate in a single model formula. We built on Ferguson & Elkie's (2004) use of polynomial regression by adding random intercepts to control for individual and annual variation in move-

ment rates, allowing us to identify up to 8 distinct biological seasons using differential calculus. Dyke (2008) obtained similar results for woodland caribou in central Canada, circumventing distributional assumptions using non-parametric LOESS (locally weighted scatterplot smoothing) curves fitted to individual time-series distributions. Disadvantages of this method include sensitivity to the choice of smoothing factor and inability to derive inflection points mathematically.

Fieberg & Delgiudice (2008) explored several methods for estimating the timing of migration in white-tailed deer using interval-censored data. For the most part, however, these approaches require advanced computing skills and are unlikely to be used by most wildlife managers (Fieberg & Delgiudice, 2008). Furthermore, time-to-event models require knowledge of when the event (e.g. migration) has occurred, which (in the case of migration) may not be possible for animals that do not have strictly defined summer and winter ranges.

Despite the prevalence of increasingly complex movement models (e.g. Smouse *et al.*, 2010), we demonstrate a relatively simple quantitative approach to defining biological seasons using iterative analyses of variance (ANOVA) and prior knowledge of species life history. Recursive partitioning works by maximizing the between-groups sums of squares along a temporal gradient; it is non-parametric and may be applied in any circumstance where changes in the movement parameter(s) of a species are known to reflect seasonal shifts in its annual life cycle. It is also fairly robust to missing values (Therneau & Atkinson, 2011), although it is best used with high-fix GPS telemetry data (≥ 1 observation/day). We do not recommend it be used without scrutiny, however, for even with smoothed data stochastic variation is likely to result in more inflection points than are biologically justified, at least at the individual level. For this reason we chose only seasons we were able to distinguish via changes in movement rates, closely supervising candidate splits and retaining only those that made sense from a biological point of view (optionally, users may increase the complexity parameter, or the minimum admissible increase in R^2 , to reduce the number of candidate splits). In parallel we also modeled changes in net displacement to support our final choice of individual onset dates for the beginning and end of spring dispersal. In a similar manner, Shuter (2011) modeled two separate movement parameters - displacement and linearity - to identify seasonal onset dates for woodland caribou in northwestern Ontario using univariate regression trees.

We recognize that many variables can influence seasonal onset behaviour in terrestrial mammals (Monteith *et al.*, 2011). Accordingly, researchers may wish to consider any number of additional explanatory variables in the model (e.g. temperature, altitude, snow depth, plant phenology, species life-history characteristics). Shuter (2011), for example, included photoperiod along with Julian day as independent variables. In the case where a fixed temporal window is deemed adequate yet individual variation is still of interest, one may consider obtaining population-level estimates (peak onset dates) using a random effects-expectation maximization (RE-EM) tree (Galimberti & Montanari, 2002; Sela & Simonoff, 2010).

Conclusion

Animals such as woodland caribou exhibit marked trends in movement behaviour that reflect seasonal variation in the relative importance of foraging, reproduction, energy conservation, and predator avoidance. For this reason the study of animal space use patterns tends to be inherently seasonal in nature. However, the timing of seasonal events in the life cycle of animals may vary considerably from year to year and/or among individuals. This raises concern as to the prudence of adopting fixed time periods in the analysis of seasonal space use behaviour (e.g. habitat selection), for they may introduce unwanted bias in the form of observations that are not strictly representative of the biological activity under investigation.

Our study provides evidence that dates determined by expert consensus and conventionally used to differentiate seasonal periods may not always be representative of the biological phenomena for which they were intended. We recommend researchers consult the biological signal of their study population using quantitative methods and other first-hand knowledge in order to verify the accuracy of the dates, and consequently the appropriateness of the data, used. Wherever possible, we also recommend varying the temporal window used to extract observations based on individually determined seasonal onset dates (e.g. Apps *et al.* 2001), for doing so should reduce misclassification and potentially erroneous bias in subsequent analyses of habitat selection.

Acknowledgements

We would like to thank our reviewers for their constructive contributions to this paper. We would also like to thank the Quebec Ministry of Natural Resources and Wildlife and the UQÀT/QÀM NSERC Industrial Chair in

Sustainable Forest Management, and the Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) - Programme Actions Concertées - Fonds Forestier for funding support. Lastly, we are grateful to Maxime Allard, Nicolas Bergeron, Vincent Brodeur, Nicolas Courbin, Stéphane Daigle, Steve Ferguson, and Robert Schneider for their contributions to this project.

References

- Apps, C., McLellan, B.N., Kinley, T., & Flaa, J.P. 2001. Scale-dependent habitat selection by mountain caribou, Columbia Mountains, British Columbia. – *Journal of Wildlife Management* 65(1): 65-77.
- Bergeron, Y., Gauthier, S., Kafka, V., Lefort, P., & Lesieur, D. 2001. Natural fire frequency for the eastern Canadian boreal forest: consequences for sustainable forestry. – *Canadian Journal of Forest Research* 31: 384-391.
- Bergerud, A.T. 1975. The reproductive season of woodland caribou. – *Canadian Journal of Zoology* 53: 1213-1221.
- Bergerud, A.T. & Page, R.E. 1987. Displacement & dispersion of parturient caribou at calving as antipredator tactics. – *Can. J. Zool.* 65: 1597-1606.
- Bradshaw, C.J.A., Sims, D.W., & Hays, G.C. 2007. Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. – *Ecological Applications* 17(2): 628-638.
- Brito, J.C. 2003. Seasonal variation in movements, home range, and habitat use by male *Vipera latastei* in northern Portugal. – *Journal of Herpetology* 37(1): 155-160.
- Brown, G.S., Mallory, F.E., & Rettie, W.J. 2003. Range size and seasonal movement for female woodland caribou in the boreal forest of northeastern Ontario. – *Rangifer Special Issue No. 14*: 227-233.
- Cameron, R.D., Smith, W.T., Fancy, S.G., Gerhart, K.L., & White, R.G. 1993. Calving success of female caribou in relation to body weight. – *Can. J. Zool.* 71: 480-486.
- Canada, E. 2008. Scientific review for the identification of critical habitat for woodland caribou (*Rangifer tarandus caribou*), boreal population, in Canada. Ottawa: Environment Canada.
- Courbin, N., Fortin, D., Dussault, C., & Courtois, R. 2009. Landscape management for woodland caribou: the protection of forest blocks influences wolf-caribou co-occurrence. – *Landscape Ecology* 24: 1375-1388.
- Courtois, R. 2003. La conservation du caribou forestier dans un contexte de perte d'habitat et de fragmentation du milieu. Montreal, Quebec. 368pp.
- Courtois, R., Bernatchez, L., Ouellet, J.-P., & Breton, L. 2003. Significance of caribou (*Rangifer tarandus*) ecotypes from a molecular genetics viewpoint. – *Conservation Genetics* 4(4): 393-404.
- Covell, D.F., Miller, D.S., & Karasov, W.H. 1996. Cost of locomotion & daily energy expenditure by free-living swift foxes (*Vulpes velox*): a seasonal comparison. – *Canadian Journal of Zoology* 74: 283-290.
- Cumming, H.G. & Beange, D.B. 1987. Dispersion and movements of woodland caribou near Lake Nipigon, Ontario. – *J. Wildl. Manage.* 51(1): 69-79.
- Clutton-Brock, T.H. & Guinness, F.E. 1975. Behaviour of the red deer (*Cervus elaphus* L.) at calving time. – *Behaviour* 55(3/4): 287-300.
- D'eon, R.G. 2003. Effects of a stationary GPS fix-rate bias on habitat-selection analyses. – *Journal of Wildlife Management* 67(4): 858-863.
- Darby, W.R. & Pruitt, W.O. 1984. Habitat use, movements and grouping behavior of woodland caribou, *Rangifer tarandus caribou*, in southeastern Manitoba. – *Can Field-Nat* 98: 184-190.
- De'ath, G. & Fabricius, K.E. 2000. Classification and regression trees: a powerful yet simple technique for ecological data analysis. – *Ecology* 81(11): 3178-3192.
- Dussault, C., Courtois, R., Ouellet, J.-P., & Huot, J. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. – *Wildlife Society Bulletin* 27: 965-972.
- Dussault, C., Courtois, R., Ouellet, J.-P., & Huot, J. 2001. Influence of satellite geometry & differential correction on GPS location accuracy. – *Wildlife Society Bulletin* 29: 171-179.
- Dyke, C. 2008. Spatial & temporal characterization of woodland caribou (*Rangifer tarandus caribou*) calving habitat in the boreal plains & boreal shield ecozones of Manitoba & Saskatchewan. M. Sc., Natural Resources Institute, Winnipeg, MB. 105pp.
- Efron, B. & Tibshirani, R. 1986. Bootstrap methods for standard errors, confidence intervals, & other measures of statistical accuracy. *Statistical Science* 1(1): 54-75.
- Eloranta, E. & Nieminen, M. 1986. Calving of the experimental reindeer herd in Kaamanen during 1970-85. – *Rangifer Special Issue No. 1*: 115-121.
- Espmark, Y. 1971. Mother-young relationship & ontogeny of behaviour in reindeer (*Rangifer tarandus* L.). – *Zeitschrift für Tierpsychologie* 29(1): 42-81.
- Fancy, S.G. & Whitten, K.R. 1991. Selection of calving sites by Porcupine herd caribou. – *Canadian Journal of Zoology* 69(7): 1736-1743.
- Ferguson, S.H. & Elkie, P.C. 2004. Seasonal movement patterns of woodland caribou (*Rangifer tarandus caribou*). – *J. Zool.* 262(2): 125-134.
- Ferguson, S.H., Rettie, W.J., & Messier, F. 1998. Fractal measures of female caribou movements. – *Rangifer Special Issue No. 10*: 139-147.
- Fieberg, J. & G. Delgiudice. 2008. Exploring Migration Data Using Interval-Censored Time-to-Event Models. *Journal of Wildlife Management* 72(5): 1211-1219.
- Flydal, K. & Reimers, E. 2002. Relationship between calving time & physical condition in three wild reindeer *Rangifer tarandus* populations in southern Norway. – *Wildlife Biology* 8: 145-151.
- Frair, J.L., Fieberg, J., Hebblewhite, M., Cagnacci, F., DeCesare, N.J., & Pedrotti, L. 2010. Resolving issues

- of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. – *Phil. Trans. R. Soc. B* 365(15): 2187–2200.
- Galimberti, G. & Montanari, A. 2002. Regression trees for longitudinal data with time-dependent covariates. In *Classification, Clustering & Data Analysis*. Springer. 508 pp.
- Garner, G.W., Knick, S.T., & Douglas, D.C. 1990. Seasonal movements of adult female polar bears in the Bering & Chukchi seas. – *Bears: Their Biology & Management* 8: 219–226.
- Gates, C.C. 1979. Effects of posture & activity on metabolic responses of wapiti to cold. – *Journal of Wildlife Management* 43(2): 564–567.
- Gillies, C.S., Hebblewhite, M., Nielsen, S.E., Krawchuk, M.A., Aldridge, C.L., Frair, J.L., Saher, D.J., Stevens, C.E., & Jerde, C.L. 2006. Application of random effects to the study of resource selection by animals. – *Journal of Animal Ecology* 75: 887–898.
- Gustafson, E.J. & Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. – *Ecology* 77: 94–107.
- Gustine, D.D. 2005. Plasticity in selection strategies of woodland caribou (*Rangifer tarandus caribou*) during winter and calving. M. Sc., Natural Resources & Environmental Studies, Prince George. 217pp.
- Hins, C., Ouellet, J.-P., Dussault, C., & St-Laurent, M.-H. 2009. Habitat selection by forest-dwelling caribou in managed boreal forest of eastern Canada: Evidence of a landscape configuration effect. – *Forest Ecology & Management* 257(2): 636–643.
- Irving, L., Krog, H., & Monson, M. 1955. The metabolism of some Alaskan animals in winter & summer. – *Physiological Zoology* 28(3): 173–185.
- Jingfors, K.T. 1982. Seasonal activity budgets & movements of a reintroduced Alaskan muskox herd. – *Journal of Wildlife Management* 46(2): 344–350.
- Johnson, C.J., Parker, K.L., & Heard, D.C. 2001. Foraging across a variable landscape: behavioral decisions made by woodland caribou at multiple spatial scales. – *Oecologia* 127.
- Johnson, C.J., Parker, K.L., Heard, D.C., & Gillingham, M.P. 2002. A multiscale behavioral approach to understanding the movements of woodland caribou. – *Ecological Applications* 12(6): 1840–1860.
- Jones, E.S., Gillingham, M.P., Seip, D.R., & Heard, D.C. 2007. Comparison of seasonal habitat selection between threatened woodland caribou ecotypes in central British Columbia. – *Rangifer Special Issue No. 17*: 111–119.
- Klein, D.R. 1982. Fire, Lichens & Caribou. – *J. Range Management* 61(1): 65–71.
- Klein, D.R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, & phenology. – *Rangifer Special Issue No. 3*: 123–130.
- Langvatn, R., Mysterud, A., Stenseth, N.C., & Yoccoz, N.G. 2004. Timing & synchrony of ovulation in red deer constrained by short northern summers. – *The American Naturalist* 163(5): 763–772.
- Lantin, É., Drapeau, P., Paré, M., & Bergeron, Y. 2003. Preliminary assessment of habitat characteristics of woodland caribou calving areas in the Claybelt region of Québec & Ontario, Canada. – *Rangifer Special Issue No. 14*: 23–27.
- Lent, P.C. 1966. Calving and related social behavior in the barren-ground caribou. – *Zeitschrift für Tierpsychologie* 23: 701–756.
- Mahoney, S.P. & Schaefer, J.A. 2002. Long-term changes in demography and migration of Newfoundland caribou. – *Journal of Mammalogy* 83(4): 957–963.
- McEwan, E.H. 1970. Energy metabolism of barren-ground caribou (*Rangifer tarandus*). – *Canadian Journal of Zoology* 48: 391–392.
- McEwan, E.H., & Whitehead, P.E. 1970. Seasonal changes in the energy and nitrogen intake in reindeer & caribou. – *Canadian Journal of Zoology* 48(5): 905–913.
- Moen, A.N. 1976. Energy conservation of white-tailed deer in the winter. – *Ecology* 192–198.
- Moen, A.N. 1978. Seasonal changes in heart rates, activity, metabolism, & forage intake of white-tailed deer. – *Journal of Wildlife Management* 42(4): 715–738.
- Monteith, K.L., Bleich, V.C., Stephenson, T.R., Pierce, B.M., Conner, M.M., Klaver, R.W., & Bowyer, R.T. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, & life-history characteristics. – *Ecosphere* 2(4): 1–34.
- Nielson, R.M., Manly, B.F.J., McDonald, L.L., Sawyer, H., & McDonald, T.L. 2009. Estimating habitat selection when GPS fix success is less than 100%. – *Ecology* 90(10): 2956–2962.
- Ozoga, J.J. & Gysel, L.W. 1972. Response of white-tailed deer to winter weather. – *Journal of Wildlife Management* 36: 892–896.
- Paré, D. & Huot, J. 1985. Seasonal movements of female caribou of the Caniapiscau region, Quebec. – In: T.C. Meredith & A.M. Martell (eds.). *Second North American Caribou Workshop*. McGill University, Montreal, pp. 47–56.
- Parker, G.R. 1981. Physical & reproductive characteristics of an expanding woodland caribou population (*Rangifer tarandus caribou*) in northern Labrador. – *Can. J. Zoology* 59: 1929–1940.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & the R Development Core Team. 2010. nlme: Linear & Nonlinear Mixed Effects Models. R package version 2.9.0.
- Post, E., Boving, P.S., Pederson, C., & MacArthur, M.A. 2003. Synchrony between caribou calving & plant phenology in depredated & non-depredated populations. – *Canadian Journal of Forest Research* 81: 1709–1714.
- Post, E. & Klein, D.R. 1999. Caribou calf production & seasonal range quality during a population decline. – *Journal of Wildlife Management* 63(1): 335–345.

- Post, E. & Stenseth, N.C. 1999. Climatic variability, plant phenology and northern ungulates. – *Ecology* 80(4): 1322-1339.
- Potvin, F. & Breton, L. 1988. Use of a net gun for capturing white-tailed deer, *Odocoileus virginianus*, on Anticosti Island, Quebec. – *Canadian Field-Naturalist* 102(4): 697-700.
- Pruitt, W.O. 1957. Observations on the bioclimate of some taiga mammals. – *Arctic* 10(3): 131-139.
- Reimers, E., Dahle, B., Eftestøl, S., Colman, J.E., & Gaare, E. 2007. Effects of a power line on migration and range use of wild reindeer. – *Biological Conservation* 134: 484-494.
- Rempel, R.S., Rodgers, A.R., & Abraham, K.F. 1995. Performance of a GPS animal location system under boreal forest canopy. – *Journal of Wildlife Management* 59(3): 543-551.
- Rettie, W.J. & Messier, F. 1998. Dynamics of woodland caribou populations at the southern limit of their range in Saskatchewan. – *Canadian Journal of Zoology* 76: 251-259.
- Rettie, W.J. & Messier, F. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. – *Ecography* 23: 466-478.
- Rettie, W.J. & Messier, F. 2001. Range use & movement rates of woodland caribou in Saskatchewan. – *Canadian Journal of Zoology* 79(11): 1933-1940.
- Rudolph, T. D. 2011. Spring dispersal & habitat selection of boreal caribou in Northern Quebec. M.Sc. thesis, Department of biological sciences, University of Quebec in Montreal. 184pp.
- Saher, D.J. & Schmiegelow, F.A. 2005. Movement pathways and habitat selection by woodland caribou during spring migration. – *Rangifer* Special Issue No. 16: 143-154.
- Schneider, R.R., Wynes, B., Wasel, S., & Dzus, E. 2000. Rate of movement of caribou in northern Alberta relative to snow depth & time of year. Boreal Caribou Research Program.
- Sela, R.J. & Simonoff, J.S. 2010. REEMtree: Regression trees with random effects. R package version 0.82, URL <http://cran.r-project.org/web/packages/REEMtree/index.html>.
- Sharma, S., Couturier, S., & Côté, S.D. 2009. Impacts of climate change on the seasonal distribution of migratory caribou. – *Global Change Biology* 15: 2549-2562.
- Shuter, J. 2010. Movement behaviour of woodland caribou at multiple spatial scales. Ph.D. thesis, University of Guelph. 214pp.
- Smouse, P.E., Focardi, S., Moorcroft, P.R., Kie, J.G., Forrester, J.D., & Morales, J.M. 2010. Stochastic modelling of animal movement. – *Phil. Trans. R. Soc. B* 365: 2201-2211.
- St-Pierre, D., Bélanger, M., Courtois, R., & Drapeau, P. 2006. Projet de recherche sur le caribou forestier: Impacts des modalités d'intervention forestière de l'entente Québec-Cris sur le caribou forestier. Rapport d'étape. Ministère des Ressources naturelles et de la Faune, Direction de l'aménagement de la faune du Nord-du-Québec, Direction de la recherche sur la faune, Université du Québec à Montréal.
- R Core Development Team. 2010. R: A language & environment for statistical computing. Version 2.9.0. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org>.
- Telfer, E.S. & Kelsall, J.P. 1984. Adaptation of some large North American mammals for survival in snow. – *Ecology* 65: 1828-1834.
- Therneau, T. M. & Atkinson, E. J. 2011. An introduction to recursive partitioning using the RPART routines. The Mayo Foundation, 67pp.
- Therneau, T.M., Atkinson, B., & Ripley, B. 2010. rpart: Recursive partitioning. R package version 3.1-48. <http://CRAN.R-project.org/package=rpart>.
- Vander Wal, E. & A.R. Rodgers. 2009. Designating Seasonality Using Rate of Movement. – *Journal of Wildlife Management* 73(7): 1189-1196.
- Visscher, D.R. 2006. GPS measurement error and resource selection functions in a fragmented landscape. – *Ecography* 29: 458-464.
- Weladji, R.B., Klein, D.R., Holand, O., & Mysterud, A. 2002. Comparative response of *Rangifer tarandus* & other northern ungulates to climatic variability. – *Rangifer* 22(1): 33-50.
- Wood, A.J., Cowan, I.T., & Nordan, H.C. 1962. Periodicity of growth in ungulates as shown by deer of the genus *Odocoileus*. – *Canadian Journal of Zoology* 40: 593-603.

