Turning Angle and Displacement of Satellite Collared Caribou Using Correlated Random Walk Models and Fractal Analysis

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INTRODUCTION

This report is an analysis of caribou movement that considers successive caribou turning angles and caribou displacement using correlated random walk models and fractal dimension analyses. This analysis uses a similar strategy as Bergman et al. (2000) who used correlated random walk models to compare sedentary and migrational caribou of the George River herd. Satellite collar data from the Bathurst Caribou herd taken from 1997 through 2001 (Gunn et al. 2001) is used for this analysis.

METHODS

Analysis of turning angles

We first compare differences in turning angles as a function of year and season to determine if significant differences exist. Second, we used the turning angle data and movement data in a correlated random walk model which predicted displacement assuming a partially correlated but random distribution of turning angles. Differences between predicted and observed displacement were then used to determine if there was fidelity seasonal areas. Finally, fractal dimension of paths were compared for seasons and years to determine how the tortuosity of paths changed between seasons and if this difference was consistent among years of the study.

Turning angles were estimated using only successive locations of individual caribou that were 5–7 days apart. Turning angles were calculated as the clockwise angle relative to the last caribou movement trajectory (Karieva and Shigesada 1983). Using this method, the relative straightness of a path could be indexed by how close turning angles were to 0 or 360 degrees (Figure 1). The actual direction (i.e. north) is not considered using this method of estimating turning angles. The estimation of turning angles was done in SAS (SAS Institute 2000) using a modified version of White and Garrott's (1990) algorithms.
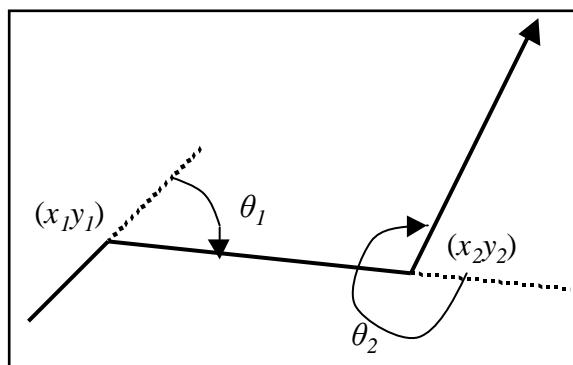

Figure 1. Parameterization of turning angles (θ) relative to successive GPS locations (x_1,y_1 and x_2,y_2).

Mean turning angles and associated variances were analyzed for individual caribou using circular statistic formulas (White and Garrott 1990) and then summarized (Zar1996) for year and season.

We also estimated an index of angular concentration. If r is close to 0 than angles are distributed randomly whereas if r=1 then all angles are identical. The Ralieghs z statistic for goodness of fit of the distribution of angles to a uniform distribution was then used to determine if the distribution of angles was non-random i.e. some type of concentration around a particular trajectory. Finally, a V-test was used to determine if the mean angle differed significantly from zero (White and Garrott 1990). A non-significant result would suggest that the caribou is going forward and turning minimally. The distribution of turning angles for year and season were also analyzed graphically to supplement test results and give a more intuitive description of difference between year and season.

Correlated random walk analysis

The correlated random walk model (Karieva and Shigesada 1983; Bergman et al. 2000) was used to generate predictions. The analysis uses the squared distance of the caribou herd from an initial starting point. For season-specific analyses, the mean location at the beginning of each season was used to estimate herd displacement. For each analysis, data was grouped by week, which allowed all locations of each animal in a herd to be considered in unison as discussed in Gunn et al. (2001). Mean displacement was then estimated as the mean of the distance of each individual animal from the initial starting point.

The correlated random walk model (Karieva and Shigesada 1983) uses the mean squared distance covered for each one week step ($E(l^2)$) and the mean distance of each step $(E(l))$, step number (n) (i.e. week of year for the year based model), and the mean of cosines of turning angles (c) to generate predicted displacement. This $E(R_n^2)$ model assumes that caribou have equal probabilities of turning left or right.

$$E(R_n^2) = nE(l^2) + 2E(l)^2 \frac{c}{1-c}\left(n - \frac{1-c^n}{1-c}\right)$$

One important aspect of this formula is how the cosine of turning angles (c) is derived.

$$c = E(\cos\theta) = \int_{-\pi}^{\pi} \cos\theta\, g(\theta)\, d(\theta)$$

In this formula $g(\theta)d(\theta)$ is the probability that an angle between two consecutive moves is between θ and $\theta+d\theta$, where θ belongs to the observed distribution of turning angles. Therefore, the degree in which the successive movements are correlated will be determined by the magnitude of the cosine of mean turning angles, which is proportional to the concentration (i.e. dispersion) of observed turning angles. Therefore, the larger the cosine

θ, the more correlated movements will be which will result in a straighter path and larger displacement. Alternatively, if cosine θ is small or 0 then a true random walk model results in which all turning angles are equally likely. Readers should refer to Karieva and Shigesada (1983) and Bergman et al. (2000) for more details on the derivation of this formula and theory behind correlated random walk models.

For the yearly analysis, mean turning angles and averaged weekly distances moved for the entire herd was input for the correlated random walk model. An empirical estimate of squared displacement was considered for an entire year using the mean location of the herd in the first of January as a starting point (as in Bergman et al. (2000)). The squared displacement of every radio collared caribou was estimated using the starting point for each week of each year and then averaged for the herd. The mean distance covered for one week $E(l)$, mean squared distance covered for each week $E(l^2)$ and the mean cosine of turning angles (c) was also estimated for each caribou (and averaged for the herd) and week combination for use in the correlated random walk model. Predicted and empirical displacements were then compared graphically.

For the seasonal analysis, correlated random walk predicted displacements were estimated for every individual in a herd and then averaged to allow an estimate of variance for the predicted correlated random walk displacements. Previous analysis suggested a large degree of variance in herd displacement potentially caused by individuals in the herd moving in an independent manner for certain seasons. If this was the case then the variance on correlated random walk predicted displacement should be relatively large. In contrast, if the herd was dispersed but still moving in a dependent manner then the correlated random walk variance should still be low compared to the variance of herd displacement (Table 1).

Table 1. Inference about herd movements and herd dispersion from the comparison of observed and predicted herd displacement variances.

	Observed variance	
Predicted (CRW) variance	**Low**	**High**
Low	Herd moving dependently Herd congregated	Herd moving dependently Herd dispersed
High	Herd moving independently Herd congregated	Herd moving independently Herd dispersed

Correlated random walk models assume that successive distances moved and successive turning angles are not auto-correlated (Turchin 1998). Therefore, detection of autocorrelation can be used to explain reasons for differences between observed and expected displacement. Autocorrelation of successive distance moved was explored using the Durbin-Watson tests for autocorrelation as part of proc AUTOREG in SAS (SAS Institute, 2000). Autocorrelation of successive turning angles was tested for using contingency type tests as

described by Turchin (1998). A Fisher exact test was used to test for significant autocorrelation given that it is more robust to low cell frequencies in contingency test tables (Agresti 1990). Analysis was stratified by year and season. Only caribou that had at least 10 successive moves were used in the analysis.

Fractal analysis estimates the tortuosity of caribou movement paths that is relatively unaffected by immediate scale of measurement. A fractal dimension of one is a straight line whereas a fractal dimension of two constitutes Brownian motion with continuous turns (Nams submitted). Therefore, the tortuosity of path segments can be compared between individuals and seasons. For example, fractal analysis was used by Marell et al. (2002) to compare searching pattern of reindeer when confronted with different availabilities of food sources.

Fractal dimension was estimated for individual caribou for season and year combinations for all paths that had at least five continuous points. Fractal analysis was conducted using the dividers method as implemented in program FRACTAL (Nams 2003). Fractal dimension was normalized for the ANOVA analysis by log (d-1) (where d is fractal dimension) as suggested by Nams (2003).

The fractal dimensions were then tested using ANOVA to determine if there were significant differences in fractal dimension of movement between season and whether these differences were consistent for each of the years in the analysis. As an initial step, scale dependency of fractal dimension was tested by regressing the fractal dimension against spatial scale for each combination of season and path for individual caribou. A significant relationship between scale and fractal dimension would indicate that scale does affect fractal dimension making it a less robust measure of path tortuosity for the given scale of measurements (Turchin 1996). Once this was done, SAS PROC GLM was used to test for differences in seasonal or yearly fractal dimension of movements. If significant differences were detected then the LSMEANS was used to produce standardized fractal dimension estimates for seasons and years. Statistical differences between fractal dimensions were tested using Bonferroni adjusted t-tests between pairs of LS mean estimates (SAS Institute 2000).

RESULTS

Analysis of turning angles

The overall distribution of turning angles for caribou with seasons pooled is displayed as star charts (Figure 2). The outside numbers are the angles and the inside number are the frequencies of observations in each bin. Most turning angles are forward for all years of the analysis suggesting that the overall trajectory of caribou is directed in a forward trajectory.
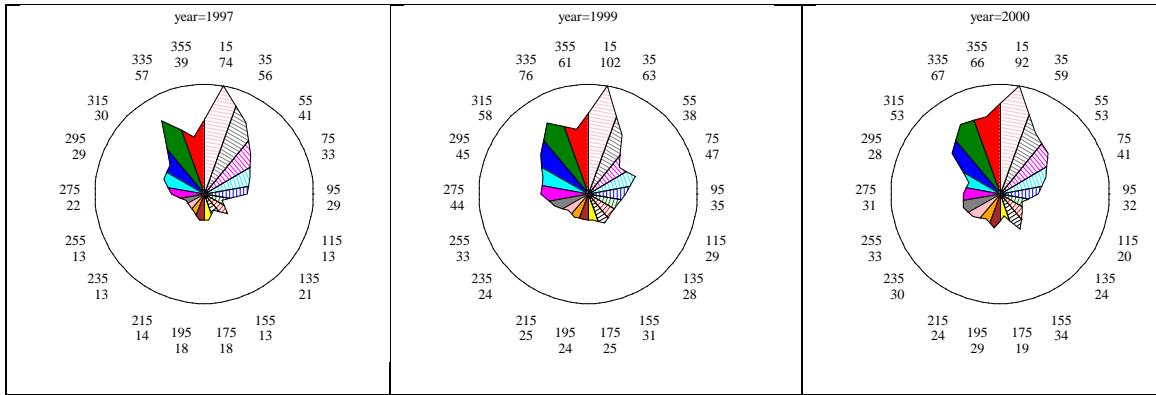
Figure 2. Pooled turning angles for each year of the analysis.

The mean turning angle and degree of variation in the distribution of turning angles varied greatly between seasons and year (Table 2). The most consistent season in terms of turning angles and deviation in turning angles was the pre-calving season. For the pre-calving season the distribution of angles was clustered (high r value) and significantly non-uniform, however, the mean turning angles was also significantly different from 0 suggesting that caribou herd was not always moving forward. The post calving period also had a higher degree of angular concentration.

Table 2. Mean turning angle statistics.

Year	Mean angle	Standard deviation	r	Test for uniformity		Test for mean angle =0		n
				z	p	u	p	
pre-calving								
1997	11.58	65.69	0.52	1.61	0.15	-1.76	0.04	7
1999	345.46	60.12	0.58	4.32	0.01	-2.85	0.00	14
2000	352.21	54.70	0.63	4.42	0.01	-2.95	0.00	12
2001	0.30	37.59	0.81	6.50	0.00	-3.61	0.00	11
calving								
1997	43.44	131.70	0.07	0.03	0.97	-0.18	0.43	7
1999	233.59	140.79	0.05	0.03	0.97	0.14	0.56	13
2000	322.05	124.02	0.10	0.10	0.90	-0.36	0.36	12
2001	35.26	80.86	0.37	1.23	0.26	-1.28	0.10	10
post-calving								
1997	13.76	62.83	0.55	1.80	0.12	-1.84	0.03	7
1999	339.77	93.64	0.26	0.76	0.44	-1.16	0.12	12
2000	347.86	65.41	0.52	3.26	0.03	-2.50	0.01	13
2001	351.51	76.20	0.41	1.54	0.18	-1.73	0.04	10
summer								
1997	5.85	96.11	0.24	0.42	0.63	-0.91	0.18	8
1999	19.24	104.69	0.19	0.43	0.64	-0.87	0.19	13
2000	4.97	76.03	0.41	1.89	0.13	-1.94	0.03	12
2001	34.67	101.36	0.21	0.35	0.69	-0.69	0.25	9
rut								
1997	8.54	70.69	0.47	1.31	0.22	-1.60	0.05	7
1999	346.46	50.97	0.67	4.98	0.00	-3.07	0.00	12
2000	181.57	101.90	0.21	0.42	0.64	0.92	0.82	11
2001	344.31	73.16	0.44	1.18	0.26	-1.48	0.07	7
winter								
1997	358.19	91.71	0.28	0.54	0.55	-1.04	0.15	8
1999	342.67	101.35	0.21	0.70	0.48	-1.13	0.13	17
2000	358.28	103.11	0.20	0.47	0.61	-0.97	0.17	13
2001	33.28	109.72	0.16	0.26	0.76	-0.60	0.28	11

The most intuitive way to view distributions of turning angles is using star charts as in Figure 3. It can be seen that the greatest degree of angular concentration was for the pre and post calving periods. This result is intuitive as the cows are migrating and have a greater tendency to go forward and have forward turning angles. In contrast, there is little angular concentration in the calving season, but some clumping of angles for some years in the summer and winter seasons.
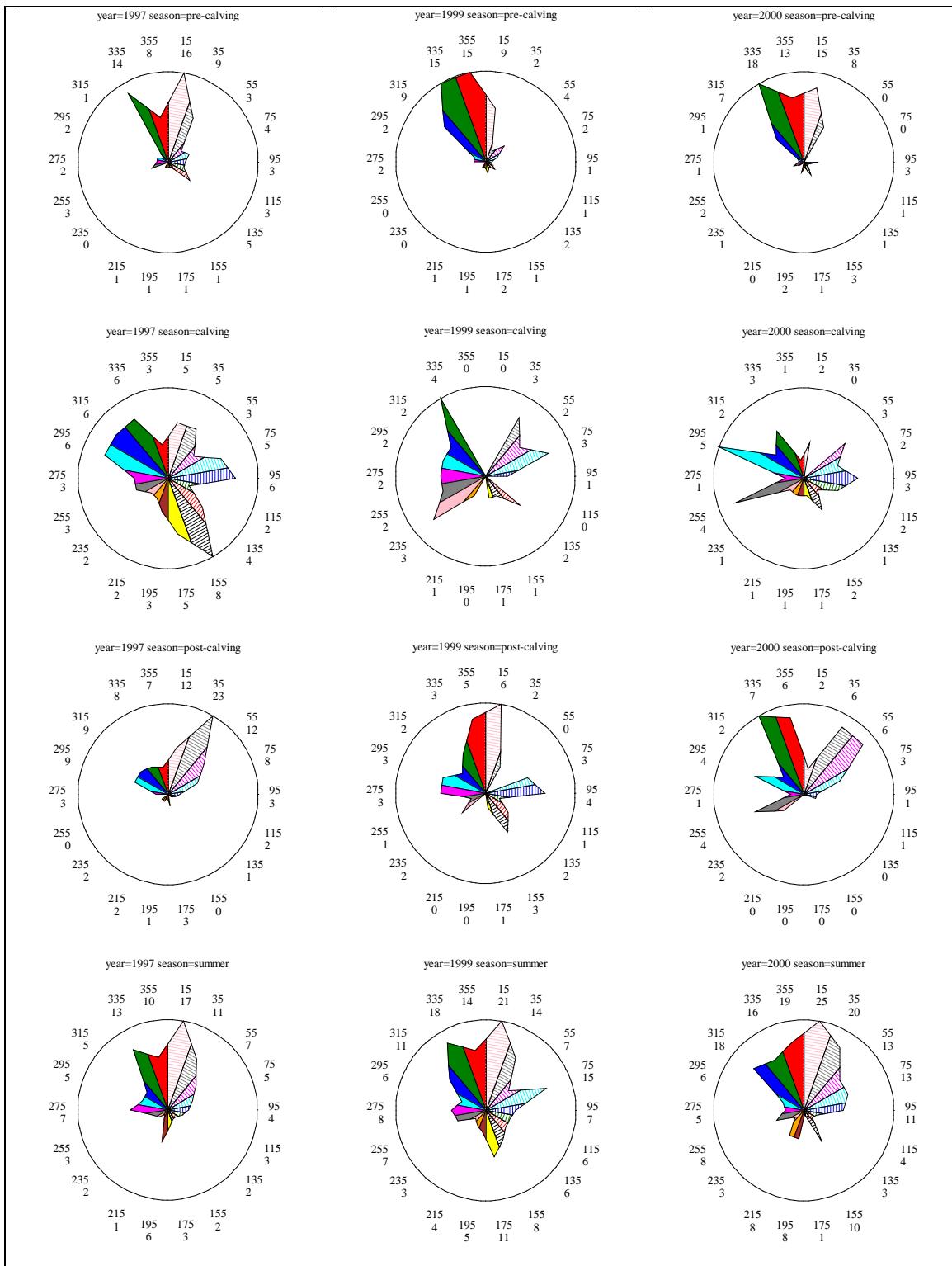
Figure 3. Distributions of turning angles by year and season. (continued on next page)
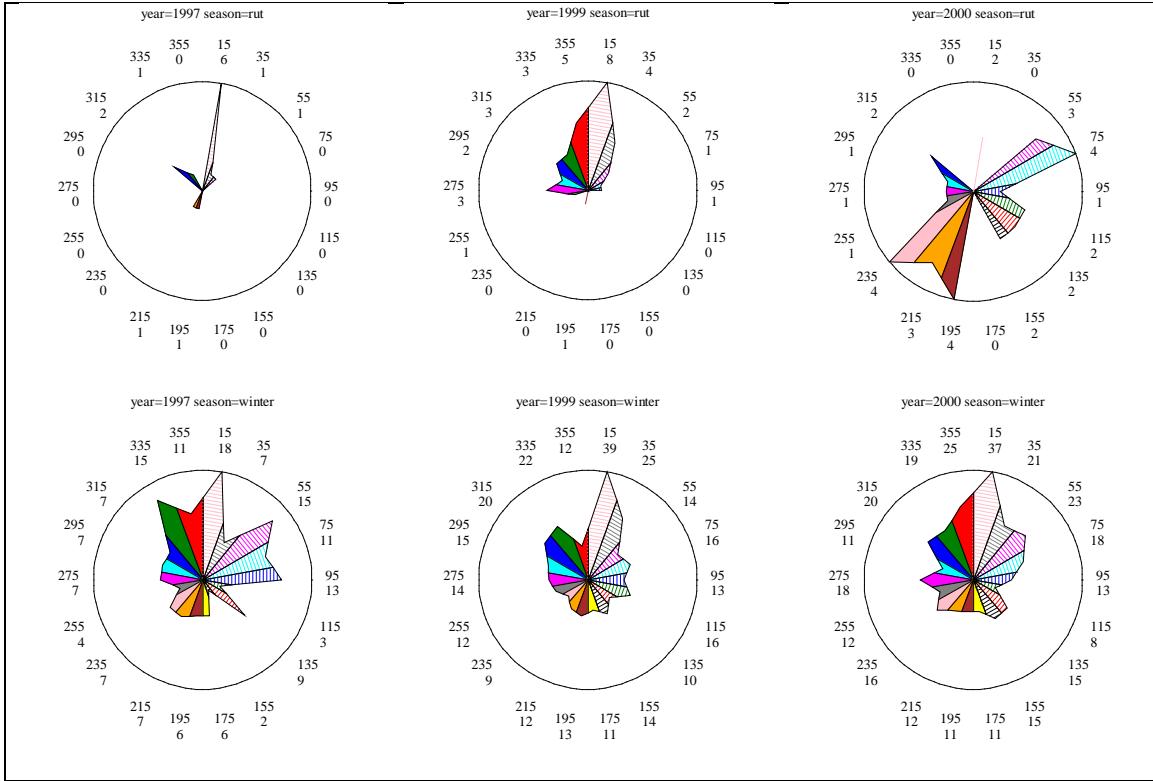
Figure 3 (continued). Distributions of turning angles by year and season.

Correlated Random Walk Model

Annual displacement

The random walk model was first used to predict displacement on an annual basis. A consistent trend was seen with general agreement or under-prediction of random walk model predictions and empirical displacement for the winter until the pre-calving season in which displacement increased and superseded random walk model predictions (Figure 4). The actual difference between random walk model predictions and empirical trajectories was dependent on the average distance between steps for any given year. For example, the average distance covered between steps in 1997 was higher and therefore the predicted displacement curve was steeper.
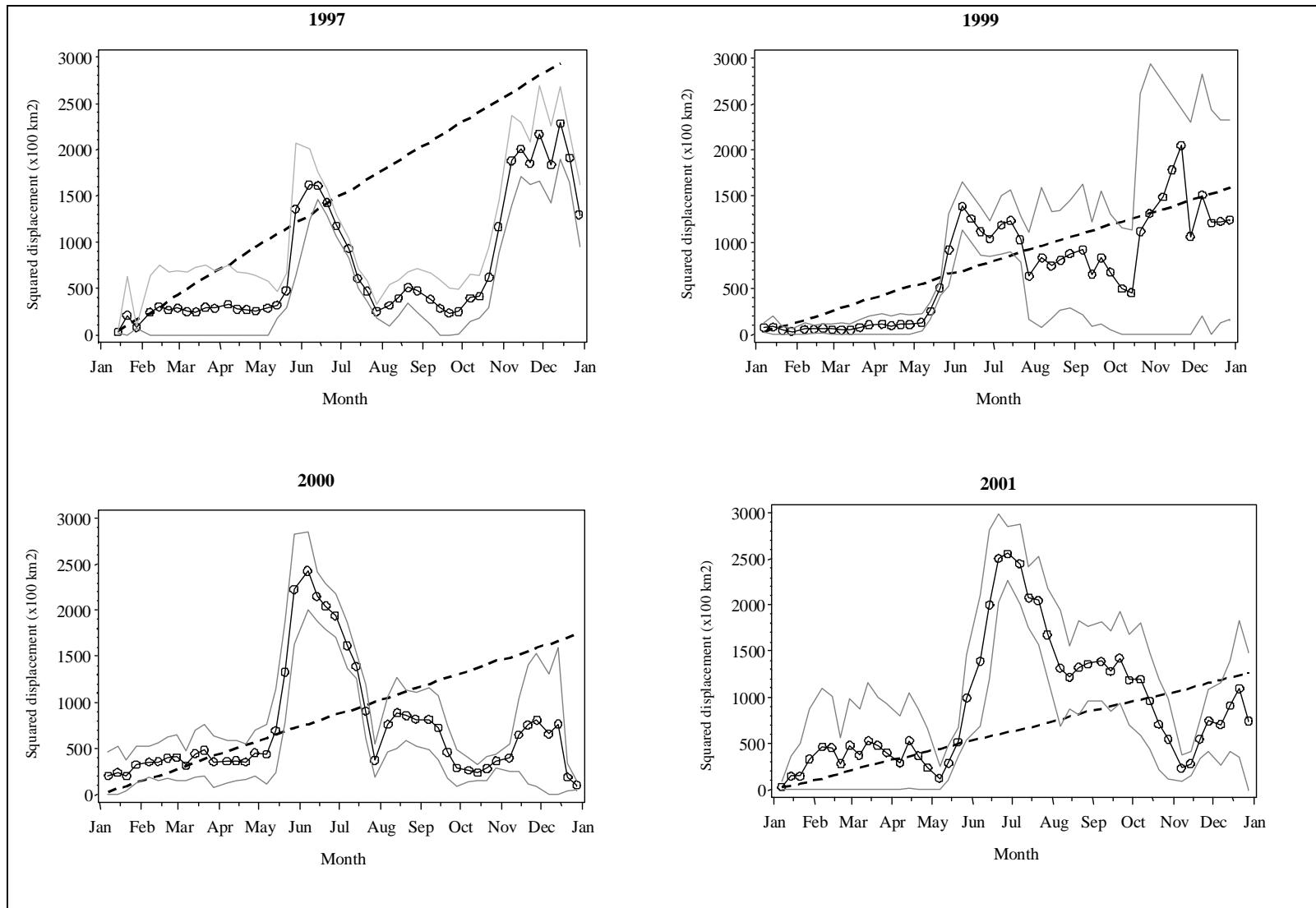
Figure 4. Annual observed and predicted displacements.

The observed trends in displacement were similar for each year considered, and also similar to the results of Bergman et al. (2000). However, the model seemed to not over predict displacement as strongly. One difficulty in making conclusion about caribou movement based upon annual displacements is that the average distance moved changes seasonally and therefore the predicted displacement from the model does not correspond to one season. Therefore, the analysis was stratified by season to allow more rigorous comparisons.

Seasonal displacement

Collar performance was poor in 1998 so this year is not presented in the analysis. In addition, there were not enough data points to allow correlated random walk analysis of the rut season.

Summer

The correlated random walk model both over and under estimated caribou displacement for the summer season (Figure 5). Displacement was overestimated for 1997 but underestimated for 1999 and 2000. In some years, such as 1996, caribou displacement was very close to predicted displacement from the correlated random walk model. Autocorrelation of successive turn angles or distances moved was detected in none of 46 animals whose paths were tested (Appendix 1). Large standard deviations around observed displacements in 2000 and 2001 suggest that the herd was not that tightly congregated. Large standard deviations around correlated random walk predictions also suggested that the herd movements were relatively independent during this season. The one exception was 1997 in which herd displacement was overestimated, and standard deviation from the correlated random walk model was relatively low and uniform. This suggests that herd movements during this season were more synchronized, and that caribou displayed a larger degree of fidelity to the summer range.
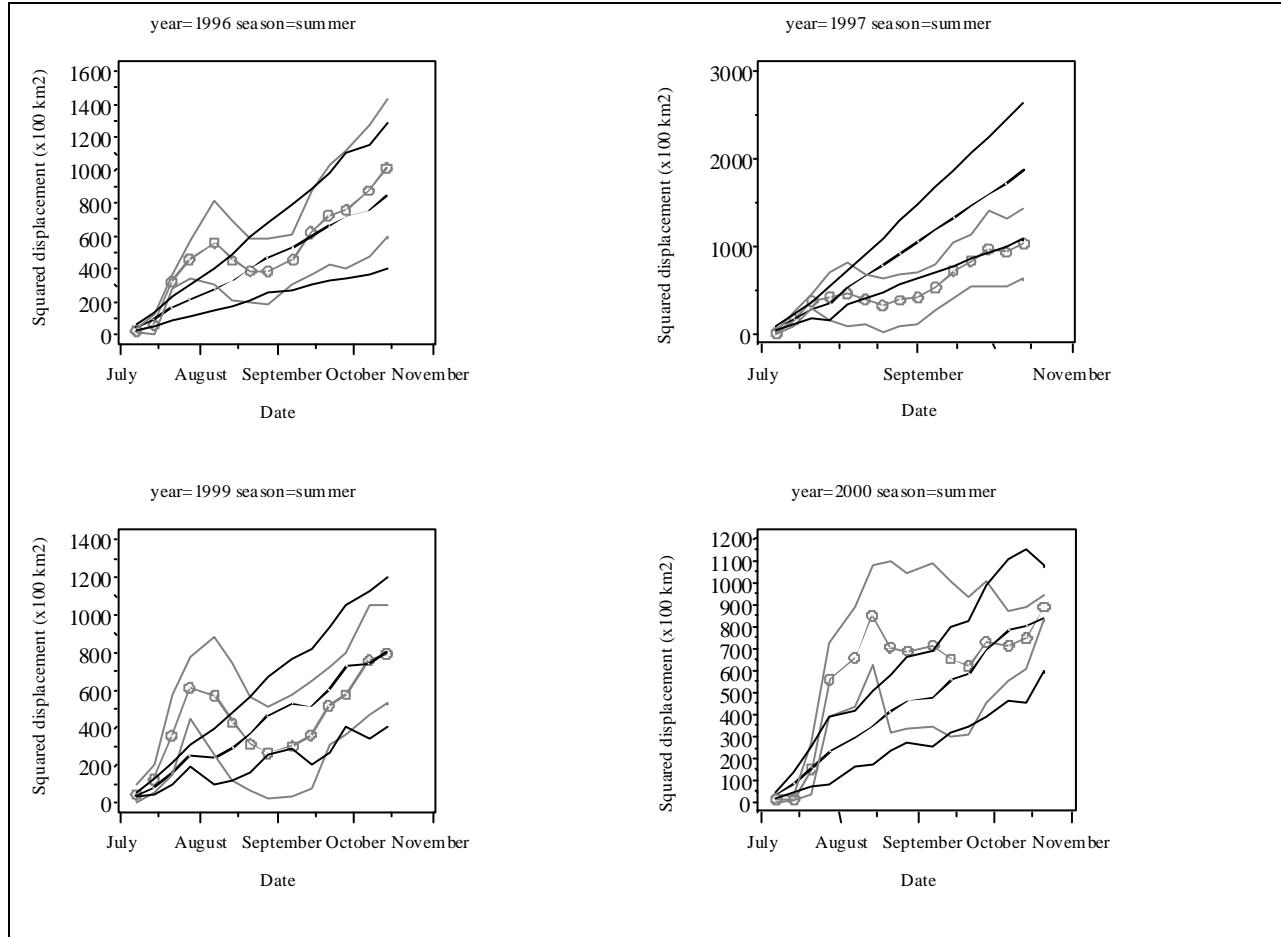
Figure 5. Observed and predicted displacement for the summer season. Solid black line shows correlated random walk predictions and associated standard deviation. Grey lines show observed displacement.

Winter

The winter period season was characterized by a large degree of variance around observed displacements suggesting a loose herd structure (Figure 6). The correlated random walk model underestimated displacement in 1999, and slightly overestimated displacement in other years. Autocorrelation of successive turn angles was only detected in 1 of 47 caribou whose paths were tested. There was no clear pattern in autocorrelation of distances moved (Appendix 1). Interestingly, the degree of variance around correlated random walk predictions was relatively low in 1999 and 2000 suggesting similar movement patterns despite the large degree of herd dispersion. In contrast, the herd displayed relatively independent movements and a high degree of dispersion during the winter of 1996.
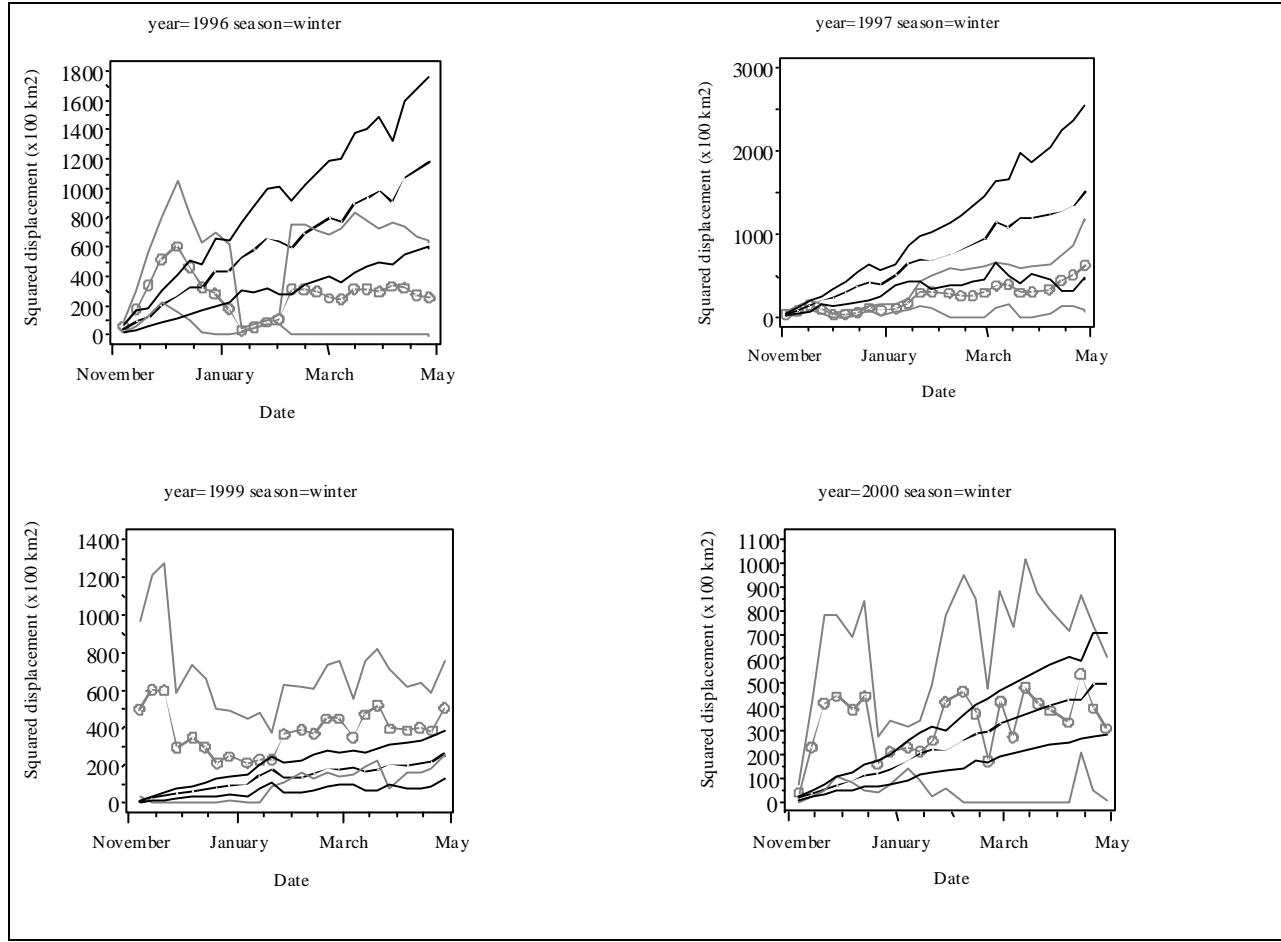
Figure 6. Observed and predicted displacement for the winter season.

Pre-calving

The correlated random walk model predictions corresponded closely to empirical displacements for the earlier dates of pre-calving seasons for all years (Figure 7). In most years the correlated random walk model slightly underestimated displacement in the latter part of the calving season suggesting a change towards more directed movements during this time. Successive distances of movement displayed negative autocorrelation in all years suggesting that the movement rate decreased as the season progressed which would also cause under prediction of displacement. Sample sizes were too low to tests for autocorrelations of successive turning angles. Standard deviations were similarly low around predicted and observed displacements suggesting that the herd was relatively well congregated and moving in a dependent fashion.
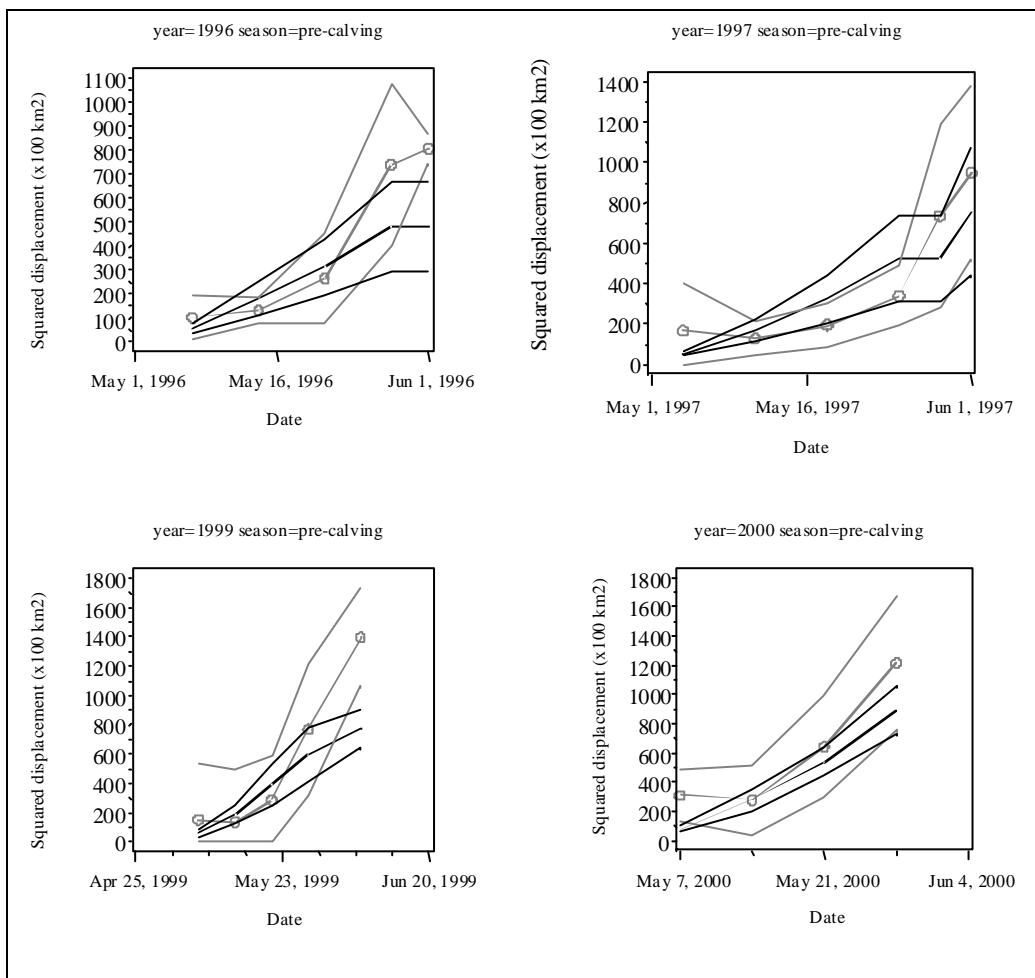
Figure 7. Observed and predicted displacement for the pre-calving season.

Calving

The calving interval was too short to include enough steps for all years except for 1996 and 1997 when collars were programmed to return daily locations. For 1996, the correlated random walk model predictions closely corresponded to observed displacements (Figure 8). In the initial part of 1997, the correlated random walk model underestimated displacement. However, as the season progressed, observed and predicted displacements became closer. The degree of variation in displacement was high initially in 1997 suggesting that a few individuals may have caused the disparity between predicted and observed trajectories. Autocorrelation of successive turn angles was not detected in 16 caribou, which is not surprising given the agreement of observed and predicted displacements. Significant positive autocorrelation of distance moved was detected in 1996 but not in 1997 (Appendix 1). The variances around correlated random walk predictions suggested that individual moves were dependent and similar.
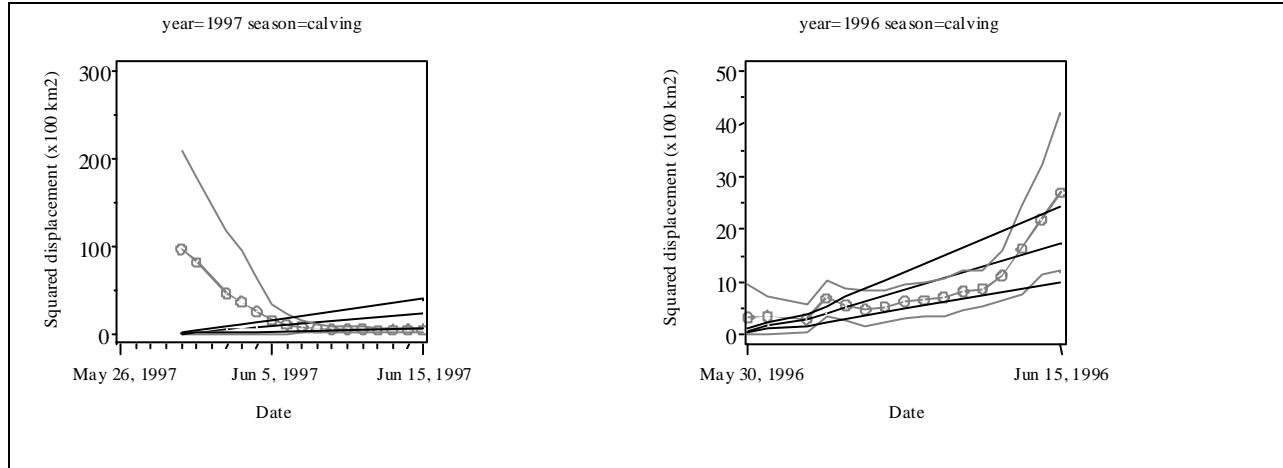
Figure 8. Observed and predicted displacement for the calving season.

Post-calving

There were only enough locations to compare observed and predicted displacements for 1996 and 1997 (when daily locations were returned from collars) (Figure 9). In both cases the correlated random walk model overestimated displacement-suggesting fidelity to post calving areas. Standard deviation around correlated random walk displacement was relatively low except in the later part of the 1997 calving period. Autocorrelation of successive turn angles or distances moved was not detected in 16 caribou whose paths were tested. At this time standard deviations of observed herd displacements also increased suggesting the herd dispersion increased.
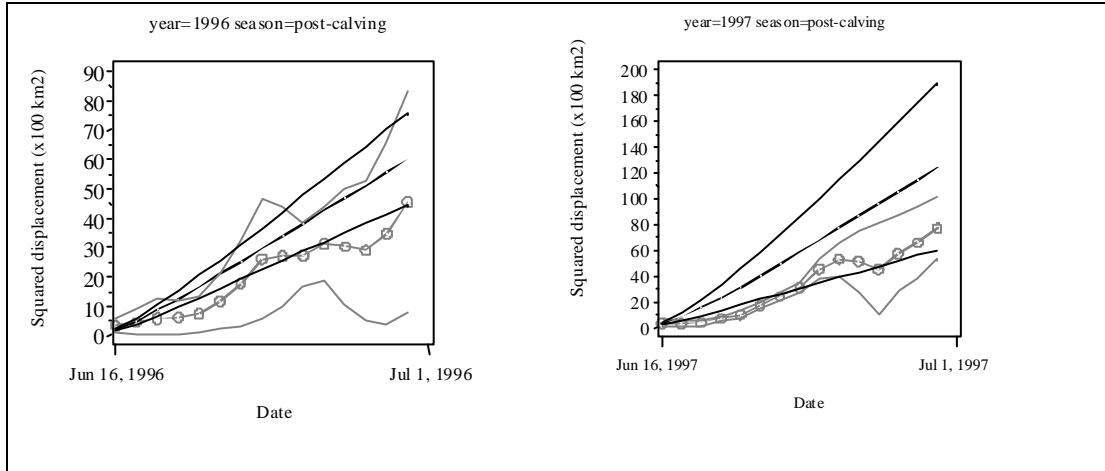
Figure 9. Observed and predicted displacement for the post-calving season.

Fractal analysis

As an initial step, the scale-dependency of fractal dimension estimates was tested by regressing fractal dimension on a spatial scale using linear regression analysis. The analysis was stratified by season under the assumption that different seasons should display different fractal dimensions. Sample sizes of paths were 18, 19, 48, 50, and 52 for the calving, post-calving, pre-calving, summer, and winter seasons. Of the analysis, there was only one scale-dependent fractal dimension measure detected in the calving

season suggesting that the measures of fractal dimension were relatively constant for the scales of measurement within each season.

One issue with the analysis was that adequate sample sizes for post-calving and calving seasons only existed for 1996 and 1997. This made it difficult to test for yearly trends and interactions between yearly trend and season using the full data set. For this reason two analyses were conducted. One analysis was conducted using all the data that determined if the fractal dimension of movements was significantly different between seasons. A second analysis was conducted in which the post-calving and calving seasons were excluded. The primary emphasis of this analysis was to determine the consistency of fractal dimensions for season and year combinations.

The first analysis for seasonal differences detected significant seasonal differences in fractal dimension (F=4.13, p=0.0045, df=4). Of the seasons, only pre-calving displayed a fractal dimension that was significantly different than other seasons (Table 3). In this case, the smaller fractal dimension suggested that movements were more linear during the pre-calving season. The most tortuous movements occurred during the post-calving season. However, the fractal dimension of post-calving movements was not significantly different than other seasons.

Table 3. Mean fractal dimension estimates and LSMEANS groupings.

Season/year	D	SE(D)	LS means group
Analysis 1-seasonal differences			
pre-calving	1.07	0.07	1
calving	1.11	0.12	2
summer	1.13	0.07	2
winter	1.15	0.07	2
post-calving	1.16	0.12	2
Analysis 2-yearly differences			
1996	1.14	0.09	1
1997	1.12	0.10	1
1999	1.11	0.07	2
2000	1.09	0.07	2

The second analysis suggested both seasonal (F=36.47, p<0.001, df=4) and yearly (F=4.49, p=0.0051, df=4) differences in fractal dimensions of movements. Seasonal estimates were similar to Analysis 1. Yearly estimates suggested that the mean fractal dimension of movements was higher in 1996 and 1997 compared to 1999 and 2000. The LSMEANS analysis suggested that these differences were statistically significant (Table 3).

DISCUSSION

Correlated Random walk

The results of this analysis suggest that the correlated random walk model is a useful tool to explore caribou movement and displacement relative to seasonal ranges. The easiest way to conceptualize the results is to consider circumstances that might lead to differences in model predictions and observed displacements. If the caribou herd is moving with no preference for right or left turns and following the mean rate and distribution of turning angles for a given season then model predictions and observed displacement should be similar. If the turning angle of the caribou herd affects the next turning angle then the turning angles will be further correlated than the model assumes leading to an underestimation of displacement. Some authors suggest that fidelity to an area as manifested by a tendency to turn back and travel in circular and non-straight paths might lead to this type of scenario. In this case successive turning angles will be auto-correlated, which allows further exploration of this type of behavior. Another potential reason for under prediction of displacement is negative autocorrelation of distances moved. For example, distances moved were negative correlated for the pre-calving season that potentially led to under prediction of displacement by the correlated random walk model.

I further modified the correlated random walk analysis to allow an estimate of variance on predicted displacement. I argue that this gives further inference on the degree of independence or dependence of movements of caribou in a herd. If caribou movements are dependent, then variance should be low. In contrast, variances should be higher if there is heterogeneity of caribou movements. One issue identified in previous analyses is that it is difficult to determine when herds are moving in a dependent or independent way. One potential reason for this is that the degree of dependence probably changes between and within seasons and therefore it is difficult to stratify a data set based upon dependence or independence. Use of correlated random walk variances allows continuous evaluation of this assumption without the need for stratification. The estimate of variance also allows further inference into the reliability of predicted random walk displacements.

Comparison of predicted and observed displacements for the summer period suggests that caribou did not show defined fidelity or avoidance of summer range areas given that the model both over and under estimated displacement. In addition variances on observed displacement were high suggesting that herds were not congregated. Large variances around correlated random walk predictions also suggested that there was heterogeneity or individual behavior in how caribou were moving. This could be due to herds breaking into sub groups or dispersing so that movements were less synchronized.

Similar trends were exhibited in the winter and summer seasons. However, in the winter of 1999, the variance around correlated random walk predictions was low despite the large dispersion of the herd as indicated by the large variance around observed displacement. This suggests that there was less heterogeneity in movement patterns despite the dispersed distribution of the herd. This could potentially have been due to weather or other larger scale events synchronizing individual movements.

One of the most interesting results is the overestimation of caribou displacement in the post-calving period. This result was also documented in Bergman et al. (2000) who suggested that the apparent fidelity and extended stay on calving grounds might be related to the avoidance of forested areas at the time of parturition.

The correspondence of correlated random walk models for the pre-calving period suggests that caribou are directed in their movement and the correlation between successive turning angles is minimal. Table 1 and Figure 3 also suggest that there is a tight distribution of turning angles as reflected by a high r value indicating a greater degree of angular concentration. Autocorrelation analysis suggests that the main reason for differences in predicted and observed displacement during this season is a negative autocorrelation of successive distance moved.

The correspondence between correlated random walk model predictions and displacement for the calving period suggests that caribou probably have a relatively undirected movement pattern during calving, as also suggested by nearly uniform distributions of turning angles (Figure 3). Basically, in this season caribou are equally likely to turn left or right and movements are not as directed.

Fractal dimensions

The fractal dimension analysis revealed that there was limited resolution in the satellite collar data to discern tortuosity of movements using fractal dimensions for all seasons. This could have been due to individual heterogeneity in movement paths creating a large degree of variance for any fractal dimension measure. In addition, there was yearly variation in fractal dimensions. Yearly variation could have been caused by heterogeneity in landscape patterns causing different movement paths dependent on the areas moved in a given year.

One potential issue with the use of fractal dimension is scale-dependency across the wide range of caribou movement spatial scales. This was partially tested for by regressing scale and fractal dimension for data from each season. However, some authors (Turchin 1996) argue that it is difficult to test for scale-dependency using the limited range of scales for any given analysis. It is argued that the correlated random walk model is a better vehicle to describe movement path, and test the assumptions underlying movements such as relatedness of turning angles and distances moved (Turchin 1996).

It is suspected that the longer time period between fixes in certain seasons reduced the resolution to discern finer scale movements (Turchin 1998). Given this, the measure of fractal dimension may be limited by the lower number of sample sizes per season combined with the long time duration between fixes. The obvious way to mitigate this issue is to increase the fix rate in seasons of most interest.

One potential application of fractal analysis would be the delineation of seasons. For example, it is possible that the mean fractal dimension of paths would change between the winter and pre-calving seasons. The main issue with this type of analysis is that it requires observation of individual caribou paths which is a difficult and laborious task given the large potential number of caribou paths taken over the many years of the study.

Both the correlated random walk and fractal analysis will be affected by heterogeneity of landscapes. The analyses conducted in this paper provide an exploration on the application of these measures to explore differences between seasons. However, no attempt has been made to explain variances in movements both between seasons, years, and individuals.

Recently, a number of techniques have been proposed to use these techniques to help explain how landscape heterogeneity affects movements. Nams and Bourgeois (submitted) used fractal analysis to separate movements of marten into two forms of tortuosity based upon breaks in fractal dimension with scale. From this, they showed how habitat selection occurs only at lesser scales compared to larger scale for marten. This type of approach could also be used with caribou to potentially separate scales at which caribou selection or aversion of areas occurs. Marell et al. (2002) used correlated random walks, fractal analysis, and RSF models to study reindeer movements relative to vegetation types. They concluded that deviations between correlated random walks were due to landscape heterogeneity as opposed to correlations in movement parameters. Etzenhouser et al. (1998) used fractal dimension to describe both landscape heterogeneity and tortuosity of animal movement paths. Using semi-domesticated animals in penned enclosures, they demonstrated a relationship between fractal dimensions of key browse species and fractal dimension of ungulate movements.

Both correlated random walks and fractal analysis could be used in unison with vegetation mapping to further explore caribou movement patterns. However, to provide more detailed results, caribou collars should be programmed to return at least daily fixes for seasons of interest. It is realized that programming collars to return more locations reduces the overall life of the collar therefore minimizing the usefulness of data for other applications such as survival analysis and tracking of movements over longer time periods. One potential approach would be to program a subset of collars with a higher fix rate. The results of this paper suggest that there was minimal difference between individuals in the terms of displacement or predicted displacement for certain seasons (i.e. pre-calving, calving and post-calving; Figures 7–9). In this case, sampling of a smaller number of caribou may be a reasonable representation of overall caribou herd movements. This approach would therefore allow more detailed inference about movements in critical seasons without sacrificing overall research objectives for the satellite collar data.

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APPENDIX 1: Autocorrelation Estimates for Distances Moved

Season	Year	Autocorrelation estimates at successive time lags[1]										
		1		2		3		4		5		
		$\bar{x}$	$\bar{s}$	$\bar{x}$	$\bar{s}$	$\bar{x}$	$\bar{s}$	$\bar{x}$	$\bar{s}$	$\bar{x}$	$\bar{s}$	n
calving	1996	*0.34*	0.05	*0.15*	0.07	-0.02	0.04	*-0.13*	0.02	*-0.18*	0.05	9
	1997	0.22	0.11	-0.04	0.13	-0.08	0.07	-0.11	0.11	-0.11	0.07	7
post-calving	1996	0.01	0.07	-0.08	0.08	*-0.17*	0.06	-0.07	0.05	0.04	0.10	9
	1997	0.07	0.09	-0.20	0.09	-0.17	0.10	*-0.22*	0.06	-0.07	0.06	7
pre-calving	1996	*-0.28*	0.09	*-0.36*	0.10	0.11	0.06	0.00	0.07	0.03	0.03	9
	1997	*-0.29*	0.06	-0.19	0.09	-0.09	0.06	-0.02	0.09	0.09	0.06	7
	1999	-0.20	0.10	-0.17	0.08	-0.07	0.08	0.05	0.04	0.01	0.05	10
	2000	-0.01	0.07	-0.39	0.06	-0.20	0.11	-0.01	0.05	0.03	0.06	11
summer	1996	0.19	0.10	-0.01	0.07	-0.10	0.07	-0.12	0.07	-0.21	0.03	9
	1997	0.04	0.07	0.07	0.08	-0.13	0.06	*-0.19*	0.06	-0.14	0.06	7
	1999	0.15	0.07	-0.03	0.06	-0.03	0.06	-0.16	0.06	-0.16	0.05	12
	2000	0.20	0.04	-0.08	0.08	-0.10	0.06	-0.15	0.05	-0.16	0.07	11
winter	1996	-0.03	0.08	*-0.34*	0.05	-0.08	0.09	-0.06	0.06	-0.03	0.04	8
	1997	0.08	0.06	-0.05	0.04	-0.08	0.04	0.00	0.03	-0.04	0.04	7
	1999	*0.13*	0.04	-0.05	0.06	-0.03	0.05	-0.02	0.05	-0.05	0.04	16

[1]Estimates in *italics* were significantly different than 0 at an α level of 0.05.