

Satellite Collaring in the Bathurst Herd of Barren-ground Caribou

1996-2005

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ABSTRACT

In 1996, the first cows in the Bathurst herd of barren-ground caribou were satellite collared. Subsequently, the program was maintained by using between five and 21 collared cows transmitting locations between 1996 and 2005. The purpose of this report is to compile information about the collaring program and the chronology of collaring. The report is an update of a 2001 summary and it is meant to be an illustrative not exhaustive review of the analyses. Satellite collared caribou locations have been used to describe seasonal and annual movements, and movement relative to three diamond mines in the NWT. The collared cows demonstrated fidelity to calving and post-calving ranges. The amount of overlap in seasonal ranges between consecutive years increased from calving throughout post-calving and the summer, before decreasing to be lowest during the winter. The area used during calving was annually the smallest and most variable in size compared to the other seasonal life history ranges. No trend was apparent in the size of the ranges between 1996 and 2005, although the southern boundary of the winter range appears to have contracted northward since 2002. Individual movement rates were more synchronized during pre-calving, calving, and post-calving and more variable in the summer and fall with an increase in movement in the time of the fall rut (mid-October to November). Average movement rates dropped from a high of 16 km/day in early summer to 4 km/day in winter.

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INTRODUCTION

The first satellite collars in the Bathurst herd of barren-ground caribou, *Rangifer tarandus groenlandicus*, were fitted in March 1996 after two years of community consultation. The capture and release of caribou was frequently said to be disrespectful and there were concerns about the effects of the collars and handling on the caribou. Some concerns about the collars were based on previous experiences. One such example was from 1979, when 202 caribou were fitted with plastic-coated fabric collars (Heard 1984) and one of the caribou was injured (A. Arrowmaker, pers. comm.). In 1996, the environmental assessment for the first diamond mine was underway and, given concerns about the effects of the mine on the caribou, there was limited support for a small number (10) of satellite collars to be fitted to cows.

The satellite collar project was originally set to run from 1996 to 1998. Weekly maps showing the caribou movements were well received in the communities. The program's support led to it being continued with West Kitikmeot Slave Study (WKSS) funding and at WKSS' request, a 1998–2001 proposal was amended to increase the number of satellite collars from 10 to 20. Through support from the Government of the Northwest Territories (GNWT), Department of Indian Affairs and Northern Development (DIAND), and WKSS, the project continued from 2001 to 2005, and has become part of the accepted monitoring and management of the herd (Bathurst Caribou Management Planning Committee 2004). The management plan for the Bathurst caribou herd includes annually maintaining between 10 and 20 satellite collars fitted to cows.

The initial objectives for the program in 1996 were:

1. To measure weekly movements of caribou cows on their seasonal ranges including the calving grounds;
2. To describe spring and fall migration routes;
3. To describe post-calving distribution in relation to weather and insect activity (mosquitoes and warble flies);
4. To measure how annual variation in the location of the calving grounds is influenced by snow and plant growth; and

5. To measure the densities of caribou within 10 km of each collared cow during pre-calving, calving, post-calving, pre-rut, rut, fall migration, mid- and late winter.

Between 1996 and 2005, those objectives became modified (Gunn et al. 2001), although the first two objectives persisted. Objectives three to five were modified or replaced as emphasis shifted more to the use of the data in the environmental assessment for mines.

Since 1996, there have been advances in the analysis of spatial data with rapid developments in Geographical Information Systems (GIS). Increasingly, some of those techniques have been or are being applied to the location data from the satellite collared caribou, which in turn has encouraged use of the data. Early in the project, WKSS and GNWT agreed on a data release protocol that allowed release of the location data on request to researchers. Most requests were for environmental assessment and monitoring for the mining industry (Appendix B). Additionally, within GNWT, the caribou telemetry data has been used in cooperative research on wolves and climate (Appendix B). The analyses, especially geostatistical, could also be applied to questions about seasonal fidelity and developing models to include environmental conditions.

We have previously reported the statistical analyses of the 1996 to 2000 satellite collar data to describe movements and distribution of the Bathurst herd (Gunn et al. 2001). The emphasis was on descriptive statistics (degree of dispersal and size of seasonal and annual ranges). Subsequently, we undertook analyses to apply the telemetry data in caribou management studies (Appendix C, this report; Boulanger et al. 2004a; Johnson et al. 2004, 2005; McNeill et al. 2005).

We have a particular interest in where individual cows calved. This interest is to determine if cows showed fidelity (philopatry) to specific calving grounds, which is the criterion used for assigning herd identity. Gunn and D'Hont (2003) reported in April 2001 and March 2002, collaring and subsequent calving and rut distribution of the collared cows for the Bathurst and Ahiak herds. Collaring in March 2003, October 2004, and March 2005 was covered in Gunn's (*in press*) report on Bathurst herd management studies (which also included the calving distribution of the collared cows).

The WKSS 2001 Annual Report had a preliminary analysis to describe the relationship between the 1996–2001 caribou locations and the diamond mines. This aspect was then expanded on in a more detailed analysis using 1996–2003 data to examine the effect of the diamond mines on caribou distribution (Boulanger et al. 2004b). Johnson et al. (2004, 2005) also used the satellite telemetry data for a conceptual approach to cumulative effects at the landscape scale.

We also analyzed fidelity to seasonal ranges. We describe turning angles and displacement using correlated random walk models and fractal dimension analyses to measure

seasonal movements and range use 1996–2000 (Appendix C). Another use of the satellite telemetry data (1996–2003) was to estimate death rates for the cows (summarized in Gunn et al. 2005a and Boulanger et al. 2004a).

In this report, we summarize the overall program between 1996 and 2005 and update some of the descriptive analyses that were first reported for the period 1996–2000 (Gunn et al. 2001). We describe the 1996–2005 seasonal and annual sample size (number of collared individuals and their longevity) and summarized the annual spatial variation in the size of annual and seasonal ranges. The report maps overall migration pathways, and annual and seasonal variation in rates of movement. As an example of variation in time (versus space), we describe individual and annual variation in the timing of collared caribou reaching a particular location. We have included a chronology of collaring, as descriptions of the timing and locations for collaring are scattered through several previous reports. The tracks of individual collared cows were mapped as a baseline and for reference to the other maps and analyses (Appendix D).

METHODS

Caribou capture

We used a net gun deployed from a helicopter for all the captures of caribou cows from 1996 to 2005.

Statistical analyses

In 1996, the statistical analyses first examined whether there were potential problems with the location data (Gunn et al. 2001). The first question was how the time interval between locations (duty cycle) affected the estimated movement rate. The analysis found a significant effect that led to the data being screened to remove locations when the duration between consecutive locations exceeded seven days. The second possible problem was whether the locations for an individual cow were auto-correlated, which is a common problem in the statistical analyses of telemetry data. Statistical tests (Gunn et al. 2001) indicated the individual locations could be averaged (the conventional approach).

To display trends in individual and seasonal movement rates, we used a spline analysis both for the 1996–2000 data and also the updated 1996–2005 data in this report. We also described how the satellite collared cows were dispersed relative to each other (using minimum convex polygon home range areas).

Using the 1996–2000 data, we developed a statistical test for association between insect abundance and caribou movement rates (Gunn et al. 2001). We did not repeat this analysis for the 1996–2005 data, however, as we only found a weak suggestion that mosquito and warble activity increased summer movements – the weather station sites were too removed from the caribou locations, the sample size of collared caribou was small and frequency of the locations was low (every five days).

To describe temporal variation in caribou movements, we looked at the mean and range of dates when collared caribou crossed an arbitrary line oriented northwest and southeast parallel to the long axis of the eastern shore of Contwoyto Lake.

Note that the means stated in this report are present \pm standard error unless otherwise noted.

Satellite collared cows as representative of the herd's distribution

We first assessed whether the satellite collared cows represented the herd using the definition of a herd as being based on the cows' return to a traditional calving ground. Herds overlap in their winter distribution so we had no means of confirming the individual cow's herd identity during capture, and therefore, we used the June distribution to assign herd identity.

We then examined whether the satellite collared cows were representative of the herd's seasonal distribution. This was an objective that had been included in the 1996 and 1998

proposals for satellite collaring. For logistical reasons, we were mostly limited to the season when dispersal of the cows was least (calving). During the 1996 and 2003 calving ground censuses, we compared the distribution of the collared cows to the mapped distribution of all cows.

In June 1997, we did not map the overall calving distribution. We determined whether the satellite collared caribou were with other caribou (that the presence of the collars did not cause avoidance) by surveying the density of caribou in the vicinity of the collared cows immediately before, during and after the peak of calving. We flew four 10-km transects (0.8 km total width) at 90° to each other and intersecting at the approximate position of the collared cow. This cross design gave us four samples radiating out 10 km at 90° from each collared cow. We used VHF radio tracking to locate the cow, but did not attempt to get a visual so as to minimize disturbance.

In 2002, an objective for the June aerial survey was to determine whether the satellite collared cows were representative of the herd's calving distribution. The criteria were that the distribution of collared cows was within the distribution of cows with calves observed during the aerial survey, and that the densities within 10 km of the collared cows, using the survey design described for 1997, were within the range of densities measured on the calving grounds.

In March 2000, we took advantage of a low-coverage reconnaissance survey of the winter range to compare the distribution of the satellite collared cows to concentrations of caribou. We flew east-west transects in a Cessna 337 to map caribou distribution.

RESULTS

Caribou capture

The capture and collaring dates, locations and details are reported elsewhere (Gunn et al. 2001, 2002; Gunn and D'Hont 2003; Gunn *in press*). The following chronology summarizes collaring in the Bathurst caribou herd.

1996: In April 1996, we located caribou using a fixed-wing aircraft, and then called a helicopter capture crew to the caribou to fit 10 Telonics ST14 satellite collars.

1998: In early April 1998, the six surviving cows collared in 1996 were scattered south and east of Great Slave Lake. The extensive distribution and VHF radio-tracking difficulties hindered collar replacement. Two 1996 collars were removed and replaced with new collars, as the two cows were in good shape and showed no wear around their necks from wearing a collar. Eight new collars were fitted to cows on 23 and 24 April 1998, resulting in 10 cows being collared in April 1998. One more 1996 collar was retrieved from a cow that was killed by a wolf before April 1998 and three more 1996 collars were removed during captures in April, June and October 1998. We were not able to recapture one cow (Cow 7766) and her collar fitted in 1996 was still transmitting in 2001, although intermittently.

Data quality from the collars fitted in April 1998 was poor, as the collars' transmissions were not well synchronized with the satellite overpasses. In October 1998, we re-caught seven of the 10 cows collared in April (we had retrieved collars from two cows that had died). We fitted five with new collars and captured and collared an additional two caribou. We reset the April 1998 collars and verified their transmission time before capturing ten cows in October 1998 and fitted them with the reset April 1998 collars.

Between 1996 and 1998, each ST14 transmitter was programmed to transmit daily during calving and early post-calving and at weekly intervals for the remainder of the year. In 1998, we switched to using ST10 collars. Compared to ST14s, the ST10s were less bulky and lighter as they used smaller batteries, although they tended to provide less accurate locations. To gain the maximum battery duration each transmitter was programmed to transmit for six hours at five-day intervals throughout the year.

2000: Eleven of the 17 cows collared in October 1998 were alive in October 2000 with their collars transmitting. As the collars were two years old, we attempted to retrieve them, however, the VHF signals were either too weak or had failed and the capture crew was unable to recapture the caribou in October 2000.

2001: In late March 2001, we attempted again to retrieve the October 1998 collars. We located the collared caribou from the satellite signals, but they were on lakes with too many other caribou and, after we had caught and replaced only one 1998 collar with a new one, further attempts were abandoned to reduce stress. In March 2001, although we were unable to

recapture the 1998 collared cows, we did capture a cow in the vicinity of the 1998 collared cows (Gunn and D'Hont, 2003) and we fitted nine new collars (including the one re-collared 1998 cow). After the problem in October 2000 of not being able to remove collars, we relied on recent developments in collar technology and used pre-programmed VHF transmitters to extend battery life and collars fitted with remote breakaway mechanisms.

2002: There was an overlap in the wintering distribution in 2000/01 southeast of Great Slave Lake between the Ahiak and Bathurst herds, which meant that we put collars on some Ahiak cows during collaring that year and had fewer satellite collars on the Bathurst herd for monitoring caribou distribution relative to mining and other activities. Thus, in March 2002, we collared a further 11 caribou cows northwest of Great Slave Lake (Gunn and D'Hont 2003).

2003: The capture crew flew to the vicinity of four of the eight existing satellite collars northwest of Gameti and deployed 10 collars in March 2003. Based on their locations in June 2003, three were Bluenose East and six were Bathurst cows (one died in April 2003).

2004: In 2004, to reduce the loss of collars to neighboring herds caused by overlapping winter distribution, we switched to collaring immediately before the rut (Gunn, *in press*). In September 2004, we flew a fixed wing reconnaissance survey to find the caribou, as the 2003 collar drop-off mechanism had worked. The drop-off mechanism had been programmed to release the collars before freeze-up to reduce the chances of the collars being lost on lakes before they could be retrieved. By June 2005, of the nine cows collared south of Wekweeti in October 2004, three died during the winter and six migrated to the Bathurst herd's calving grounds. We had also fitted two collars north of Wekweeti from a separate caribou movement and they subsequently migrated north to the Bluenose East herd's calving grounds in June 2005.

2005: We returned to collaring in late winter in 2005 as the objective included collaring in the neighbouring herds. We used fixed-wing reconnaissance surveys to cover the Bathurst herd's winter range and the western winter range of the Ahiak herd, as we also had 10 satellite collars destined for that herd. In March 2005, we coordinated with Sahtu and Inuvik regional staff (Northwest Territories Department of Environment and Natural Resources), who were mapping caribou distribution also in preparation for collaring caribou. We collared 10 cows northwest of Gameti. Of those 10 collars, three died (in April and May) and the surviving seven migrated to the Bathurst calving ground. We collared 10 cows east of Great Slave Lake and, based on the June 2005 distribution of the collared cows, eight cows were from the Ahiak herd and two were from the Bathurst herd.

Sample size

Annual and seasonal sample sizes varied from a low of three collars in 1998 (the result of poor transmission rather than the actual number of collared caribou) to a high of 21 in 1998 (Table 1, Appendix A).

Table 1. Annual and seasonal sample sizes of individual satellite collared cows, Bathurst caribou herd, April 1996 to May 2005.

Season	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005
winter	9	8	6	19	14	15	15	15	8	20
spring migration	10	7	14	16	13	14	12	13	7	17
calving	9	7	3	14	13	13	11	12	6	
post-calving	10	7	9	12	13	13	11	11	6	
early summer	9	7	8	12	12	12	11	10	5	
mid-late summer	10	8	8	13	13	13	11	10	5	
fall migration	10	7	6	14	12	11	9	10	6	
rut and late fall	9	7	21	14	13	9	10	9	10	

Annual and seasonal areas used

We used minimum convex polygons to measure the extent of area used by the satellite collared cows as a representation of annual and seasonal range use. We included all individuals rather than treating any as outliers. Thus, the mapped annual ranges could be influenced by the distribution of a single individual. In the comparison of the two time periods (1996–2000 and 2000–2005) (Figure 1), for example, the movements of cow 128 in June 2000 and cow 178 in 2005 extended the annual range east. In 2005, cow 128 was radio-tracked and was a non-breeding cow traveling with young bulls; she and cow 178 both turned west and crossed Bathurst Inlet to reach the calving ground. Similarly, the extension of the range to south of Great Bear Lake was the result of a single cow wintering near Déline in 2003.

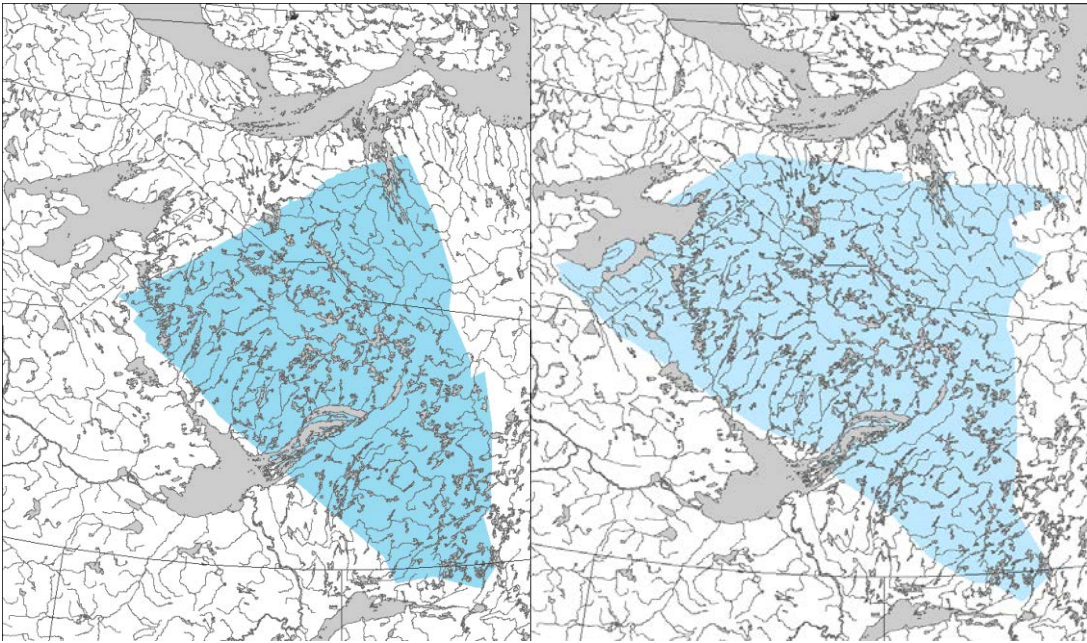


Figure 1. Annual home range based on minimum convex polygon range estimates from satellite collared cows, Bathurst caribou herd, April 1996–May 2000 (left) compared to June 2000–May 2005 (right).

Annual range size (1996–2005) based on the minimum convex polygon averaged $230,652 \pm 18,390 \text{ km}^2 \text{ SE}$ (Table 2). A linear regression of time against annual range size suggests no apparent trend between 1996 and 2005.

Table 2. Size of annual (April–March) range based on minimum convex polygon range estimates from satellite collared cows, Bathurst caribou herd, April 1996–May 2005.

Year	Area, km^2
1996/97	154,952
1997/98	218,762
1998/99	250,744
1999/00	308,735
2000/01	252,067
2001/02	220,153
2002/03	260,071
2003/04	137,192
2004/05	273,192

We also calculated seasonal ranges using minimum convex polygons on a weekly basis (Figures 2 and 3) and by life history phase (Table 3). The size of the area reflects how dispersed

the collared cows were in each month. The cows were least dispersed during calving, post calving and (except 1999) during the time of the fall rut. Most years showed similar degrees of dispersion with the exception of 1998, 1999, and 2002/03 winter (Figures 2 and 3), which had a greater amount of dispersion in the summer and fall (1999) and fall into winter (1998). Summer 2001 also stands out with the caribou being more dispersed during spring migration and mid-summer.

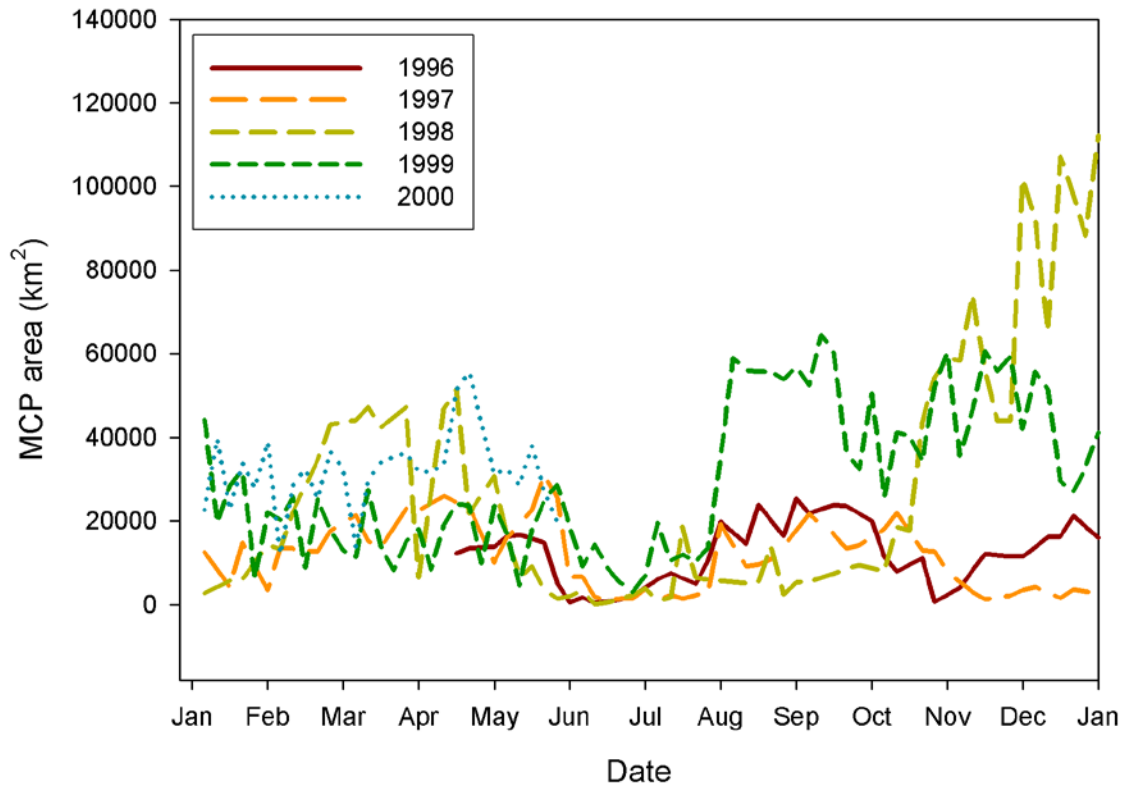


Figure 2. Seasonal area used based on minimum convex polygon range estimates from satellite collared cows, Bathurst caribou herd, April 1996–May 2000.

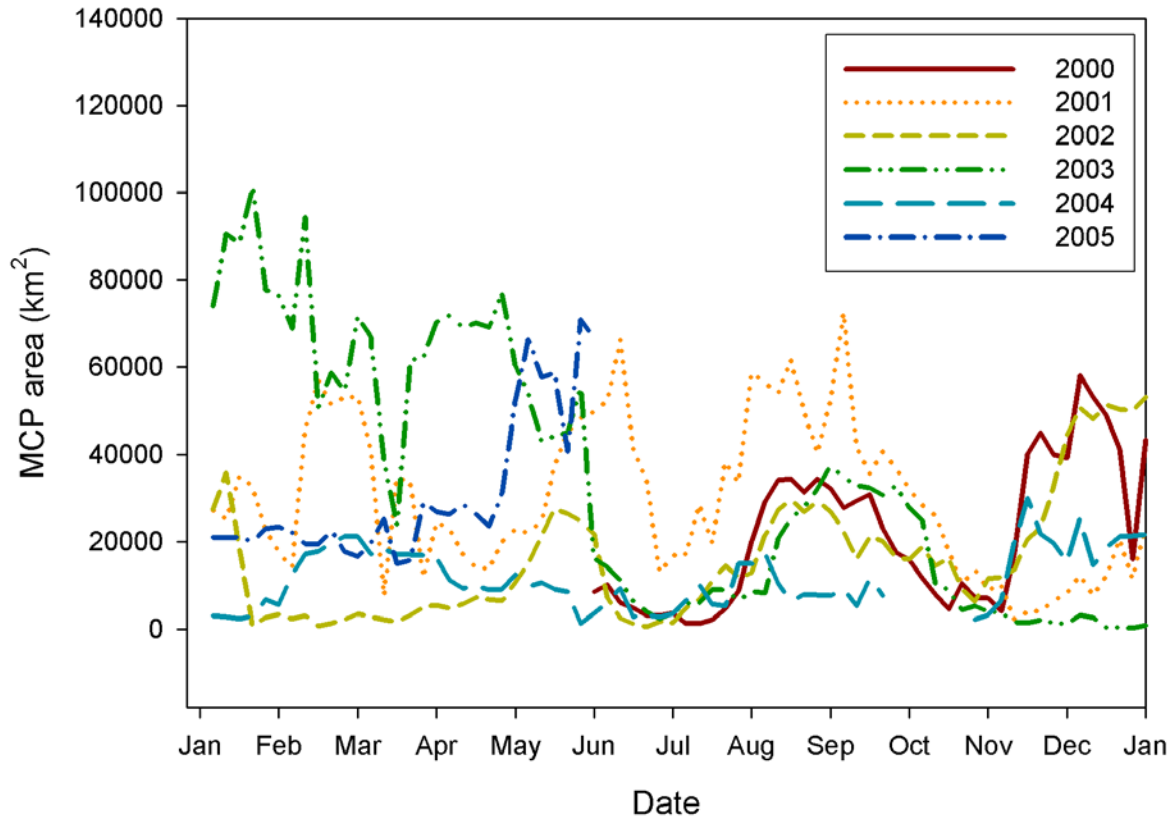


Figure 3. Seasonal area used based on minimum convex polygon range estimates from satellite collared cows, Bathurst caribou herd, May 2000–May 2005.

The amount of overlap between consecutive years increases from calving throughout post-calving and the summer before decreasing to be lowest during the winter (Table 3). The size of the area used during calving is annually the smallest and the most variable in size (coefficient of variation of 56%) compared to the other seasonal life history ranges (coefficients of variation of 13% to 26%). The two largest areas were those used during migration, both during the spring and rut/fall migration.

Table 3. Size of seasonal area used and annual overlap based on minimum convex polygon range estimates from satellite collared cows, Bathurst caribou herd, April 1996–May 2005.

Season	Start	Finish	Mean area, km ²	Min	Max	% overlap
Calving	3 Jun	13 Jun	14,400 ± 8,018	899	77,081	48.6 ± 14.0
Post-calving	14 Jun	5 Jul	20,100 ± 5,209	7,920	57,522	58.2 ± 10.7
Early summer	6 Jul	18 Jul	22,608 ± 4,059	8,205	49,033	49.1 ± 10.9
Mid-late summer	19 Jul	22 Aug	58,901 ± 9,011	36,273	105,406	66.5 ± 6.8
Fall migration	23 Aug	3 Oct	60,495 ± 8,168	37,022	111,713	58.9 ± 6.6
Rut and late fall	4 Oct	5 Dec	107,059 ± 18,576	48,730	193,795	47.3 ± 12.0
Winter	6 Dec	14 Apr	80,806 ± 16,866	12,287	195,434	30.8 ± 9.3
Spring migration	15 Apr	2 Jun	142,858 ± 21,063	53,707	254,891	41.1 ± 6.0

To illustrate the scale of annual variation and fidelity, we mapped the minimum convex polygons (MCP) for calving 1996–2006 (Figure 4). The angular shape of the polygons is a consequence of the movements of the individual cows. In 2005, the cows were late in reaching the calving ground; possibly because they were in poor body condition and pregnancy rates were lower than average (Gunn, *in press*). Alternatively or as well, the cows may have been in poor condition during the rut, and may have bred on a second estrus so calving would have been late. One cow had started spring migration with caribou from the Bluenose East herd before turning east to reach the Bathurst calving ground. The MCPs for the 2005 calving season contracted later in June as the cows congregated on the calving ground (Figure 5).

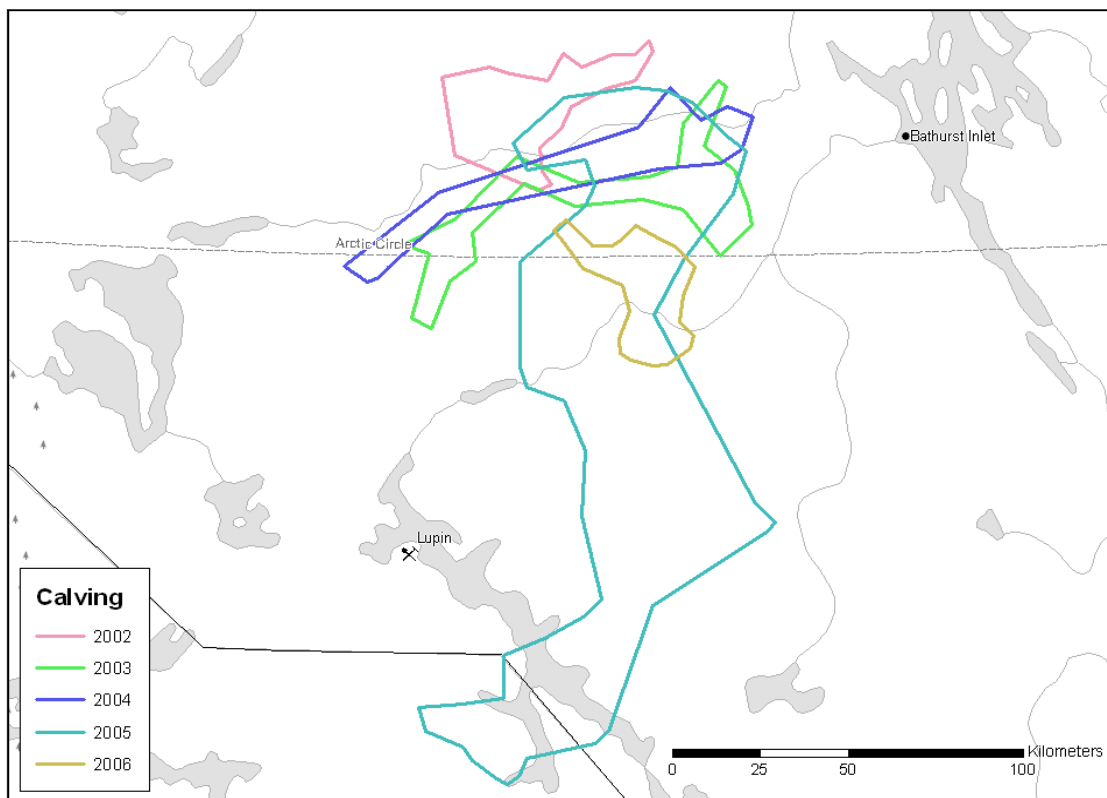
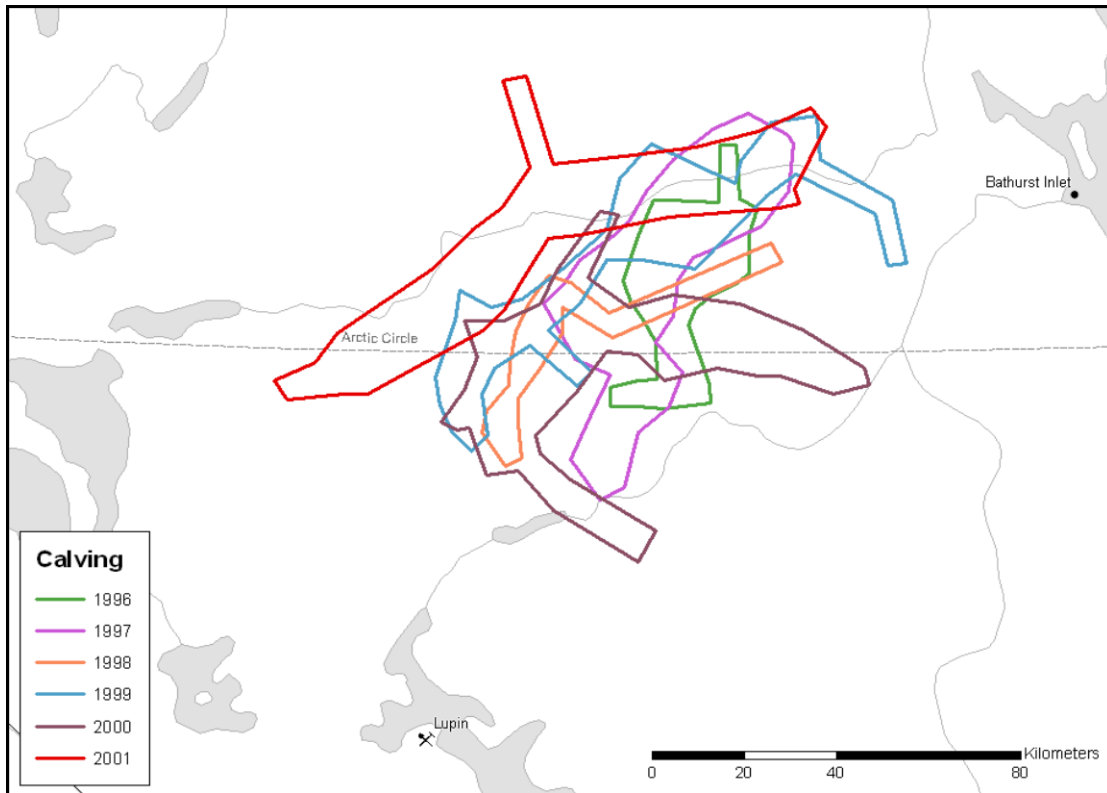


Figure 4. Minimum convex polygons for satellite collared caribou, 3–13 June 1996–2006

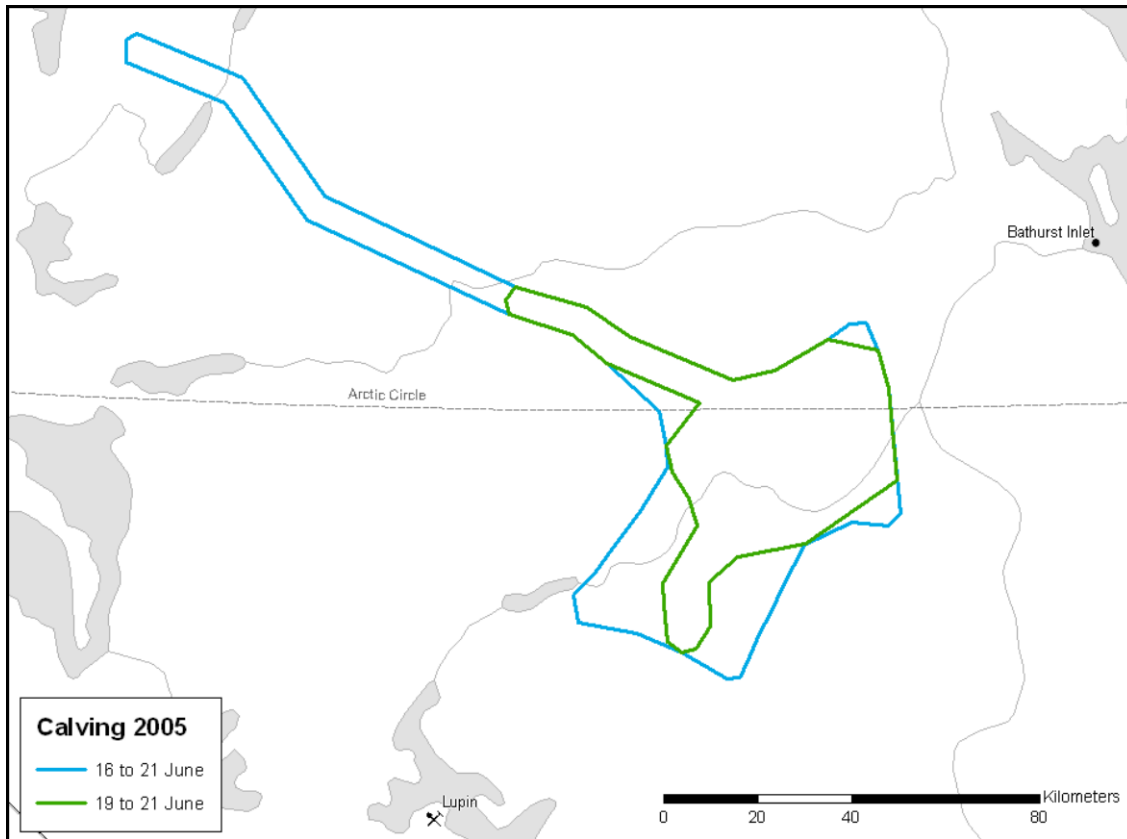


Figure 5. Minimum convex polygons for satellite collared caribou, 16–21 June 2005.

The sizes of the calving and wintering areas (based on minimum convex polygons) from 1996 to 2006 do not show significant trends over time, however, the southern boundary of the winter range has contracted (Table 4, Figures 6 and 7).

Table 4. Minimum convex polygon areas (km²) for satellite collared caribou during calving and winter, 1996 to 2006.

Calving (3–13 June)		Winter (6 Dec–14 Apr)	
1996	890	1996/97	38,151
1997	1,760	1997/98	45,339
1998	550	1998/99	67,119
1999	1,613	1998/99	14,648
2000	1,986	1999/00	37,324
2001	2,101	1999/00	28,314
2002	1,137	2000/01	74,582
2003	1,358	2001/02	35,759
2004	1,325	2002/03	36,543
2005 ^a	2,131	2003/04	26,682
2006	820	2004/05	34,760

^a16–21 June for 2005

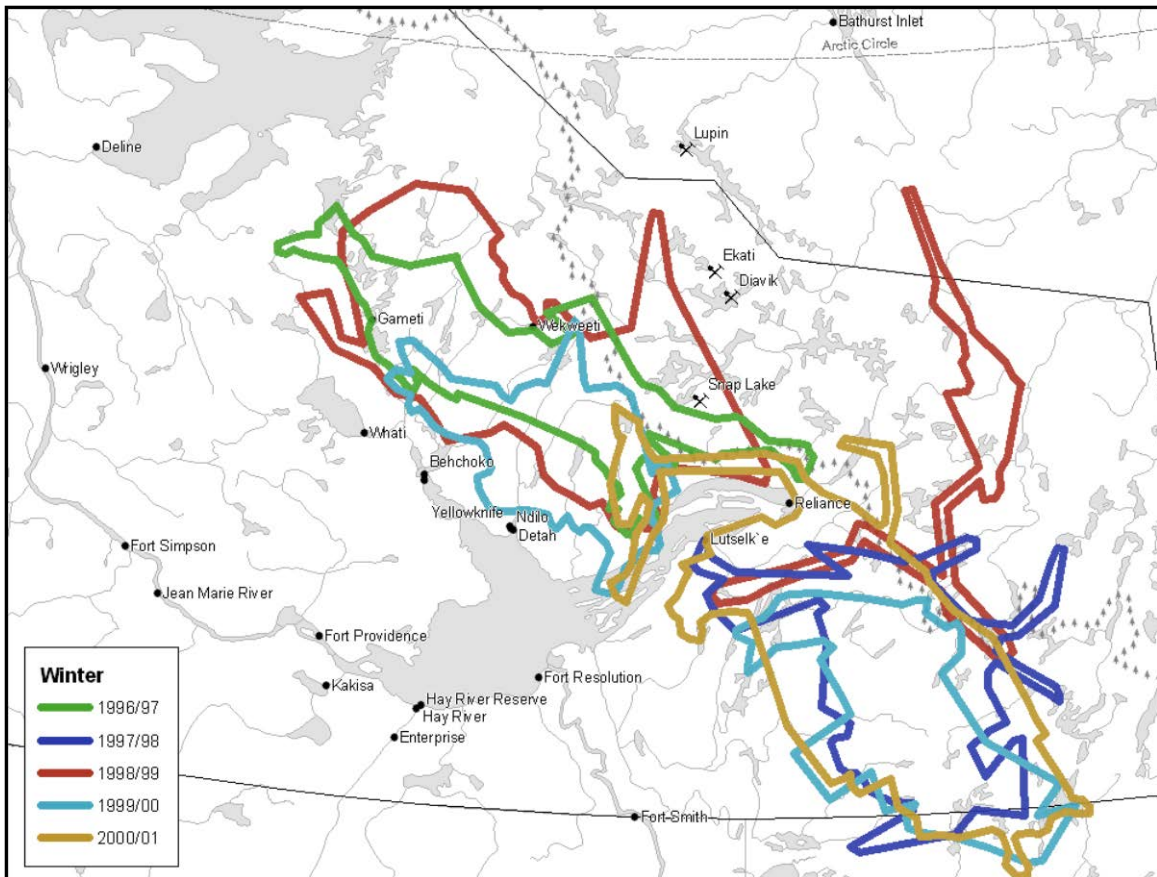


Figure 6. Minimum convex polygons for satellite collared caribou in winter, 6 December -14 April, 1996 to 2001.

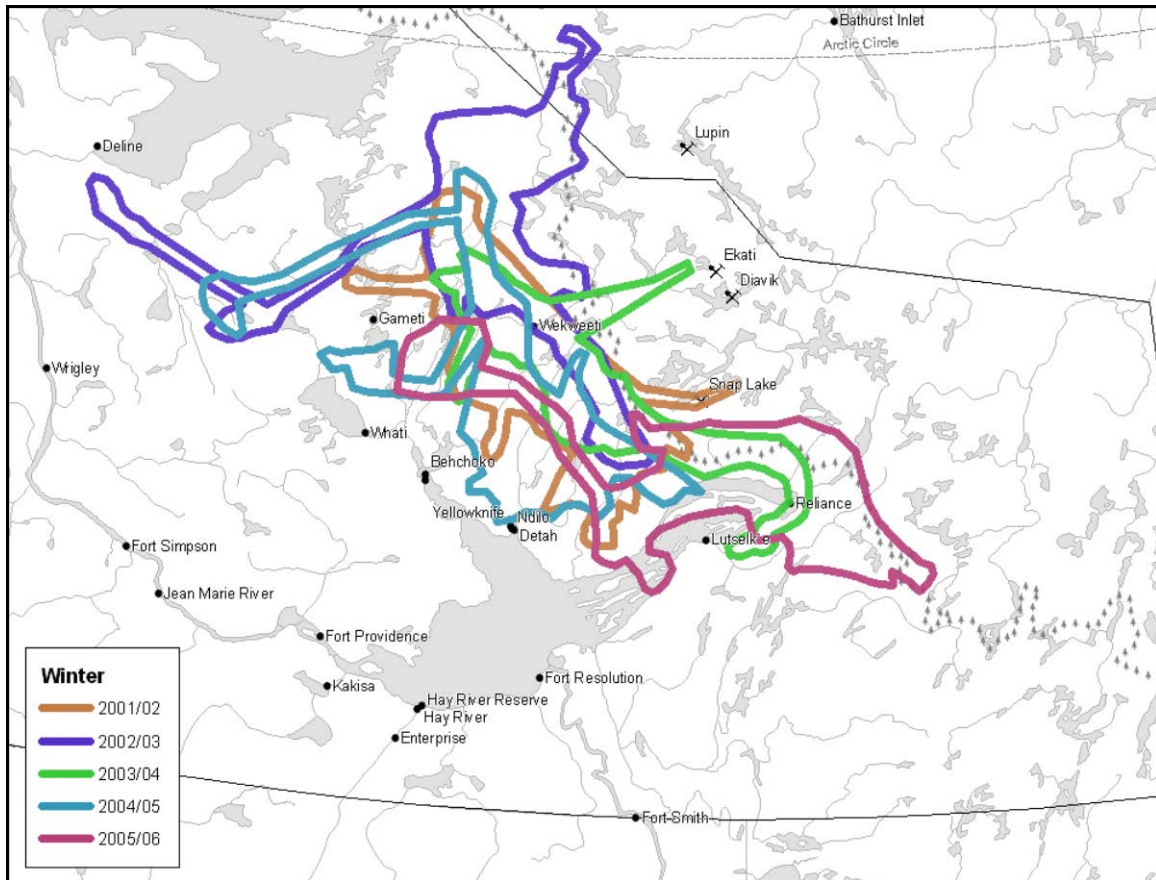


Figure 7. Minimum convex polygons for satellite collared caribou in winter, 6 December -14 April, 2001 to 2006.

Annual and seasonal movement rates

Movement rates varied between years (Figure 8). The three periods when movement rates are lowest are during calving, fall and winter (Figure 8 and Table 5). Caribou movement rates changed as a function of distance from the calving grounds: rates were higher when caribou were farther from the calving grounds and lower when closer to the calving grounds. Summer 2004, stands out as having higher rates of movements.

The May 1999 spike in movement rates (Figure 8) was from Cow 105 who traveled 233 km over seven days. She was the only collared cow to winter south of Great Slave Lake in Nonacho-Gagnon Lakes vicinity. The following year, a spike on 5 April 2000 is the same cow; her rate is inflated as she had the only seven-day duty cycle collar - all others had five-day duty cycles. She went 114.5 km over seven days.

The mean daily movement rates (Table 5) were lowest in winter. Movement rates were also low in August and September when the caribou were feeding to regain body condition after warble fly and mosquito harassment ceased. Movement rates were also low during calving and increased during post-calving into mid-late summer when insect harassment peaks.

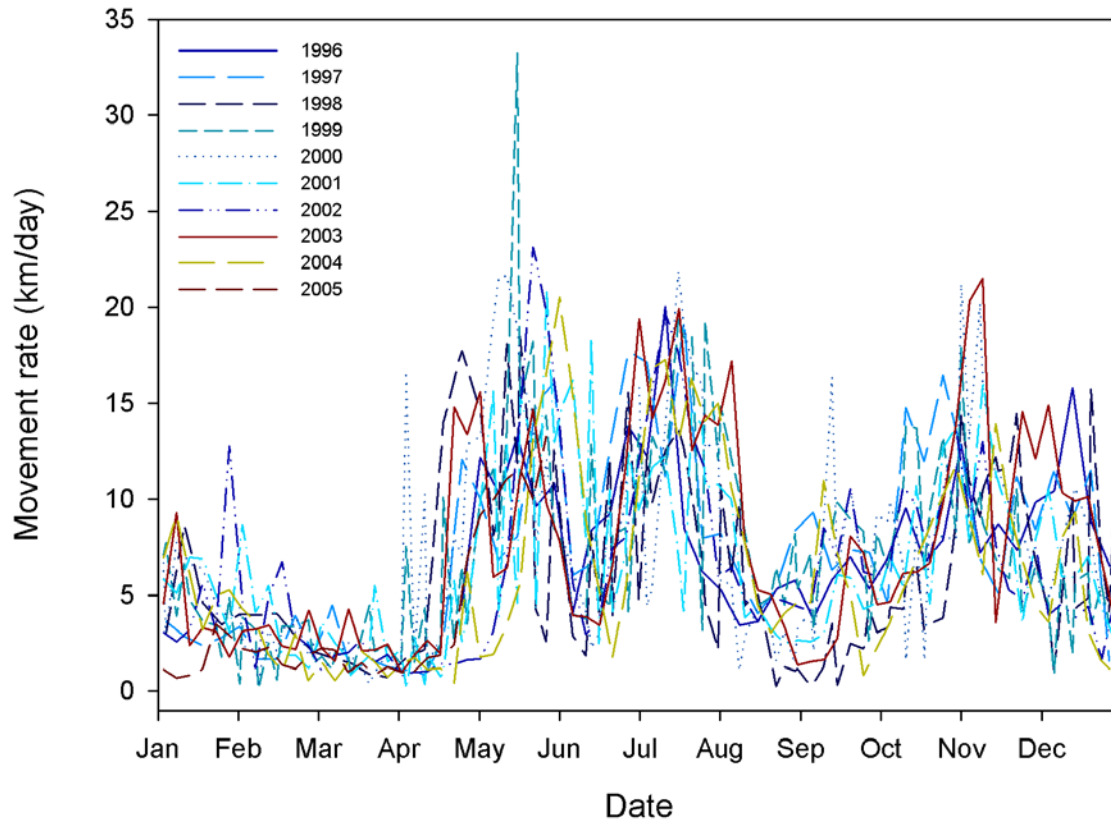


Figure 8. Mean weekly movement rates for satellite collared cows, Bathurst caribou herd, April 1996 to May 2005.

Table 5. Mean weekly movement rates by season for satellite collared cows, Bathurst caribou herd, April 1996 - May 2005. The mean is the average of all movement records for that time period.

Season	Start date	End date	Mean km/day \pm SD
calving	3-Jun	13-Jun	6.8 \pm 6.52
post-calving	14-Jun	5-Jul	10.6 \pm 7.58
early summer	6-Jul	18-Jul	15.9 \pm 8.86
mid-late summer	19-Jul	22-Aug	9.9 \pm 8.51
fall migration	23-Aug	3-Oct	5.8 \pm 5.50
rut and late fall	4-Oct	5-Dec	9.6 \pm 6.93
winter	6-Dec	14-Apr	3.6 \pm 4.33
spring migration	15-Apr	2-Jun	10.0 \pm 8.59

Migration Corridors

We used three-day average and T-spline maps to describe the annual average migration corridor for each life history phase and year. Dominating features of the composite map for 1996-2005 (Figure 9) are the relatively straight north-south spring and post-calving migrations,

compared to the more sweeping northeast-southwest loops of rut, late fall and winter movements. The rut movements are also roughly parallel to the tree line.

The composite map of movement routes for the nine years is a construct – a relative abstraction and simplification that does not include variation between individuals and years (see Appendix E for annual maps of three-day moving average and T-spline with 60 tension for satellite collared cows with the individual tracks to illustrate individual variation by year).

To illustrate temporal variation in caribou reaching a particular location, we looked at the range in dates when caribou crossed an arbitrarily chosen line parallel to Contwoyto Lake and the long axis of the extent of calving area. During pre-calving migration, the annual range of dates when the first cow migrating north crossed the line was over a 38-day period (21 April to 29 May) and 16 days (16 May to 2 June) for the time period over which the last cow crossed the line (Table 6). Between 1996 and 2004, the number of days between the first and last collared cow crossing the line averaged 21 ± 10 days (Standard Deviation).

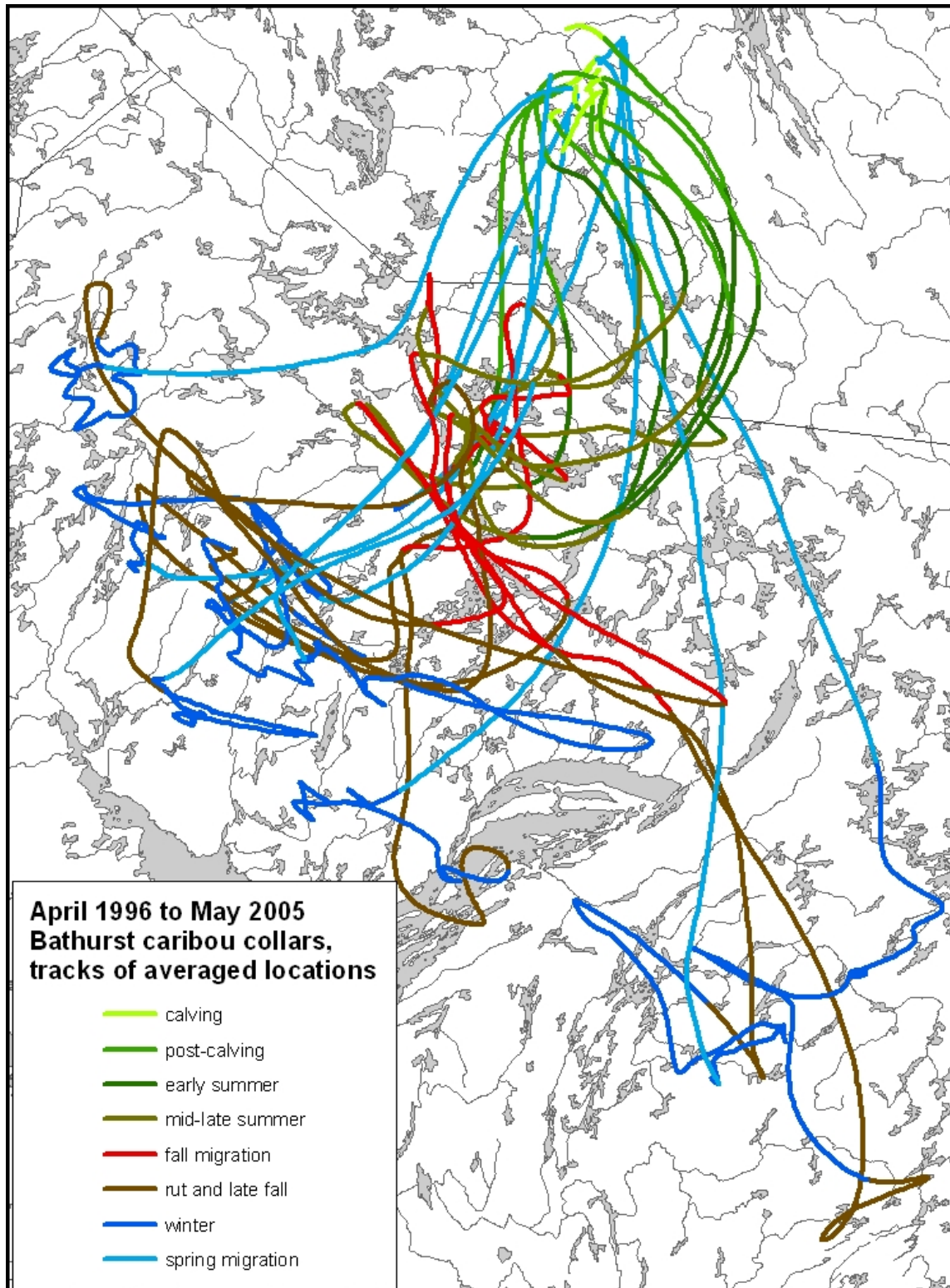


Figure 9. Overall map of 3-day moving average and T-spline with 60 tension for satellite collared cows, Bathurst caribou herd, April 1996 - May 2005.

Table 6. Sample size and range of dates when satellite collared cows, Bathurst caribou herd, crossed a line parallel to the eastern shore of Contwoyto Lake 1996 to 2004.

	1996	1997	1998	1999	2000	2001	2002	2003	2004
No. collars	9	6	6	12	13	13	8	11	2
Earliest date	2/05	11/05	27/04	4/05	26/04	16/05	16/05	21/04	29/05
Latest date	23/05	31/05	16/05	29/05	23/05	2/06	31/05	1/06	31/05

The date of the first collared cow crossing and the number of days until the last cow crossed were negatively related (linear regression $r^2 = 0.63$) – the later the date of the first cow crossing, the shorter the time interval until the last cow crossed.

Satellite collared cows as representative of the herd's distribution

Between 1996 and 2004, we had 37 individual collared cows with more than one year's calving locations. Most (78%) had two or three years of calving locations and 22% had four to six years of calving locations. We saw no collared cows that did not reach the Bathurst herd's calving ground each year or that moved to another herd's calving ground.

For the calving period in 1996, 1997, 2002, and 2003, we addressed the question of whether or not the satellite collared cows were representative of the herd's distribution. On the calving ground in June 1996, eight of nine satellite collared cows were within the area that we estimated held 82% of the caribou on the calving ground with an average density of 111 caribou/km². The ninth cow was three km north of the stratum boundary and in an area where there were a few caribou (Gunn et al. 1997).

In June 1997, we determined that the collared caribou were with other calving caribou, as we monitored the numbers of caribou in the vicinity of the collared cows by radio-tracking them and counting the caribou around them. The mean densities (caribou/km²) decreased from 22 ± 18.3 (Standard Error) during pre-calving to 9 ± 7.0 (SE) during the peak of calving when the cows were the most dispersed. After calving, the cows started to congregate and the densities around each collared cow increased to 18 ± 13.9 SE.

In 2002, the movements for 10 of 11 collared Bathurst herd cows from 4–15 June took them inside the polygon enclosing the distribution of cows with calves based on an aerial survey on 9–11 June, and the eleventh cow moved to within five km north of the polygon.

In the Ahiak herd, five of six collared cows were within the polygon enclosing the distribution of cows with calves in the eastern survey block by 14 June 2002. The sixth cow was within one km of the eastern boundary.

As noted in Gunn and D'Hont (2003), the difficulties with VHF radio tracking limited our efforts to compare densities measured during the aerial survey in the immediate vicinity of the collared cows to six collared cows in June 2002. The densities within 10 km of collared cows were higher than the overall densities in the survey blocks.

Although systematic reconnaissance surveys in late winter were not designed to test whether the satellite collared cows represented the herd's distribution, their results are illustrative. In March 2000, we flew 40 hours along east-west lines from southeast of Great Bear Lake to southeast of Great Slave Lake in a Cessna 337 between 24 and 30 March 2000 and we identified 12 concentrations of caribou (100 to 46,000 caribou). Based on the satellite locations for the closest date, nine collared cows were within four of the concentrations of caribou, two collared cows were in the immediate vicinity of concentrations and three collared cows were in areas with scattered caribou and many caribou tracks. The three eastern concentrations of caribou were not represented by a satellite collared cow.

DISCUSSION

Satellite telemetry, through its ability to record the location of an identifiable individual caribou without restrictions of distance or weather, has given us unprecedented opportunities. At the scale of the individual, we can measure movement rates, turning angles and survival rates. The point locations allow us to map distribution, the extent of which can be measured overtime (using, for example, kernels and minimum convex polygons).

To date, most of its applications have been for management studies and geared toward letting hunters and the public know the whereabouts of the caribou. Less progress has been made using satellite telemetry to investigate evolutionary strategies, for example. How caribou use space to acquire forage and avoid predation and parasites is key to their success. For example, Bergerud (1974) and Bergerud and Page (1987) have described caribou use of space to reduce risk of predation. Folstad et al. (1991) argued that caribou during post-calving migrations were spacing themselves away from parasites. However, the seasonal shifts between dispersal and aggregation behaviour are likely more complex than responses to predation and parasitism – for example, Gunn and D’Hont (2003) suggested that “public information” (*sensu* Doligez et al. 2002) about resources exchanged between aggregated caribou could have an evolutionary advantage. Questions arising from those ideas have yet to be explored using satellite telemetry.

One of the most conspicuous gaps in theoretical caribou ecology is in our knowledge of dispersal whether innate or environmental (Caughley 1977). This is not surprising – for example, Caughley (1977) commented that “dispersal is the most difficult of all population processes to investigate”. We do not yet have a theoretical framework for dispersal in caribou which means the tests and criteria for measuring it are lacking. Using telemetry retroactively to identify possible examples of dispersal is unlikely to lead to unequivocal evidence. For example, retroactive interpretation of dispersal from telemetry is handicapped by inadequate sampling of individuals across a range of sex and age classes and by not having previously established criteria for what constitutes dispersal. The use of telemetry in effectively contributing to the theory of dispersal in caribou will require some carefully designed research with an appropriate sampling design.

We used satellite telemetry to demonstrate philopatry (seasonal range fidelity) in adult females to calving and post-calving/summer ranges. Pregnancy rates averaged about 80% for adult females. We observed slower rates of spring migration in some cows that, when visually checked, were identified as non-breeders (no hard antlers and new antler growth in early June). Although they had lower rates of movement, they did reach the calving ground. The demonstrated fidelity to a calving ground supports the current criterion for identification of herds (as defined by the cow’s return to a traditional calving ground; Thomas 1969). We have found cows together during calving that are also close together during the rut.

A striking feature of the use of satellite telemetry has been that we have been able to see collared cows from a shared winter range starting migration together, then separating with an abrupt change in direction and heading to different calving grounds. For example, Figure 3 in Gunn and D'Hont (2003) shows cow 78 traveling with collared Ahiak herd cows from the winter range in 2001 before veering northwest to the Bathurst herd's calving ground where she was in June 2001, 2002, and 2003. Similarly in 2005, a cow migrated north with other cows heading toward the Ahiak herd's calving grounds before she turned west and crossed Bathurst Inlet to the Bathurst herd's current calving ground. Also in 2005, two cows migrated north on the east side of Great Bear Lake with other collared cows moving to the Bluenose East calving grounds before turning east and reaching the Bathurst herd's calving grounds in June 2005. Those abrupt changes suggest that cows have a strong fidelity to their calving ground and a "homing instinct" to that calving ground.

Although the last recorded calving ground was different from the assumed natal calving ground for 10 of 14 cows, 6 of 13 cows (one cow had only two calving locations) reversed their shift and returned to their natal calving ground. Two of the 149 cows spent an equal number of years on each calving ground (six and eight years).

In Alaska, the question of calving fidelity has been examined and questioned several times over the last three decades. A recent paper suggested that when the Mulchatna herd in the southeastern Alaska mountains was increasing, it shifted its calving ground between 1989 and 1993 over a straight-line distance of about 100 km. Hinkes et al. (2005) gave almost no details about how the shift involved overlap between 1991 and 1992 (similar to what has been recorded in the NWT). At the same time that the Mulchatna herd reached 200,000 caribou in 1996, a smaller neighbouring herd was also increasing. In 1981, the Kilbuck herd was estimated at c.50 caribou and by 1994, the estimate was 4,220 caribou. The Kilbuck herd's traditional calving ground was within 25 km of the Mulchatna's expanded calving ground. The Mulchatna and Kilbuck herds overlapped during fall 1994, and the following June, 11 of 13 collared Kilbuck cows were on the Mulchatna calving ground.

In the Bathurst herd, cows that calve together are also together during the rut, at least for the period of our data (1996–2005 and this report; Gunn and D'Hont 2003; and J. Nagy pers. Comm. for the Bluenose West, Bluenose East and Cape Bathurst herds). The only time between 1996 and 2004 when a satellite collared cow was closer to collared cows from another herd during the rut was in 1999. During mid-October 1999, cow 16565 moved southeast to an area northwest of Yellowknife where she spent the winter before returning northwest in May 2000 to the Bluenose East's calving grounds, which she had used in the previous four years (J. Nagy pers. comm.).

Although satellite telemetry of cows has not revealed overlap during the rut between barren-ground caribou herds in the NWT to date, Boulet et al. (2005) report that in Québec and Labrador, the George River and Leaf River herds have overlapped their rut distribution in seven of eight years, although the overlap was variable (average overlap $11\% \pm 12.3\%$ SD, 0.2-35%

range). Overlap during the rut is equivocal evidence for genetic exchange between herds without more evidence, such as the duration of overlap and the number of caribou associated with the satellite collared cows. Other considerations are that sample sizes of collared cows are low and that we have little data regarding how females that are not conceiving behave during the rut and during calving.

The NWT data on defining barren-ground herds is consistent in that satellite collared cows have shown fidelity to calving grounds, and cows that calve together are together during the rut. Both Hinkes et al. (2005) and Boulet et al. (2005) agree that herd identity based on calving ground fidelity is appropriate for short-term management and also suggest that a metapopulation approach may be appropriate over the longer time scale. They offer few details, however, as to the time scale and theoretical framework for dispersal strategies. The scale of immigration detected genetically is low compared to the scale that would influence abundance (so-called mass immigration): for example, Boulet et al. (2005) refer to 5–10 immigrants per generation being sufficient to explain genetic similarities between herds.

Satellite collars are only used for tracking adult females and, therefore, much remains to be learned about both juvenile and male dispersal strategies. We also know little about mate selection. A reasonable assumption is that males will have fidelity to the females in any one herd given their geographic proximity during summer and fall. In terms of evolutionary fitness, it makes 'sense' to stay within 'reach' of the females. In other members of the deer family, breeding male distribution before the rut is predicted by female distribution, and during the rut, the females also respond to the distribution of male breeding territories (references in Carranza and Valencia 1999). We can also look at breeding strategies in other members of the deer family, such as the fallow deer (*Cervus dama*) where females tend to choose males on leks near traditional routes (Apollonio et al. 1989).

Fidelity to a traditional calving ground (range) was shown based on a sample of cows for which we had information for more than one year. We observed a similar pattern of fidelity for post-calving and summer ranges, which is less well known than the fidelity to traditional calving grounds (for example Gunn and Miller 1986). Fidelity to post-calving and summer ranges is a consideration in the context of environmental assessments.

Sizes of seasonal and annual ranges in any year are the result of caribou integrating a complex set of environmental and social factors. We used minimum convex polygons to estimate the sizes of the areas used by the satellite collared cows, as it is a relatively well-accepted approach although sensitive to sample size (number of points) and bias (Burgman and Fox 2003). Among the factors affecting range use is, possibly, the numbers of caribou. However, we did not find an overall trend in the size of the annual range used by adult females between 1996 and 2005, although the size of the Bathurst herd in 2006 was half the size it was in 1996 (Nishi et al. 2008).

The application of satellite telemetry to environmental assessment has so far emphasized the distribution of satellite collared caribou relative to mine sites. The representation of those collared cows for caribou distribution has been tested by comparison with the results of aerial surveys used to monitor caribou distribution in the vicinity of the EKATI mine. The number and distance of the collared cows from the mine is predictive of caribou densities (Boulanger et al. 2004b; Rescan Environmental Services 2006).

Satellite telemetry data could be used to estimate residency time in the vicinity of the mines. This would be useful in undertaking energetics modeling for cumulative effects and risk assessment modeling for the potential effects of dust contamination of forage.

Another potential use for satellite telemetry is in developing mobile Caribou Protection Measures (CPM), such as proposed in the 2004 draft West Kitikmeot Land Use Plan. The satellite telemetry could be applied to mapping the annual extent of calving. The annual maps could be used to develop predictive maps (the probability of caribou in any one year being at a particular location). Analyses of the timing of collared caribou locations relative to fixed locations would refine the probability maps for spatial distribution. Additionally, satellite telemetry could be used to provide agencies and camp operators with current information on direction and rates of movement.

The main objective of this report was to update the descriptive statistics that were first applied to in 2001 (Gunn et al. 2001). The report has also brought under one cover the chronology of the satellite collaring. The use of the data is illustrative rather than exhaustive. Annual variation in movement rates and distribution (based on point locations) is relatively high, which means that more investigative analyses, such as caribou's evolutionary strategies on the use of space, will require an additional number of years of movement data. There is currently a decade of data, and the herd appears to have a consistent population trajectory between 1996 and 2006 (decline), which would reduce a possible source of variation in locations and rates. The time is likely appropriate to undertake more exhaustive analyses of the telemetry data to further investigate responses to industrial development, for example, and to explore other questions about the caribou cow's use of space.

ACKNOWLEDGEMENTS

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PERSONAL COMMUNICATIONS

Arrowmaker, Alex. Elder. Wekweeti, NT.

Nagy, John. Senior research biologist. Department of Environment and Natural Resources,
Inuvik, NT.

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APPENDIX A: Longevity of individual collars and seasonal sample sizes individual satellite collared cows, Bathurst caribou herd, April 1996- May 2005.

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Legend

A Active

D Programmed drop off

X Caribou recaptured & recldared with different ptt.

R Caribou recaptured and r eleased

F Ptt failure

? Cause of death unknown

W Wolf kill

G Grizzly bear kill

S Shot

?? Unknown fate - death or ptt failure

Legend
A Active
D Programmed drop off
X Caribou recaptured & recollared with different ptt.
R Caribou recaptured and released
F Ptt failure
? Cause of death unknown
W Wolf kill
G Grizzly bear kill
S Shot
?? Unknown fate - death or ptt failure

APPENDIX B: List of applicants for use of the satellite collar database for the Bathurst caribou herd and examples of the applied use of the satellite collar database for the Central Arctic Wolf Project and Climate Change Project

AMEC Americas Ltd.

Aurora Wildlife Research

BHP Billiton Diamonds Inc.

BHP Billiton World Explor. Inc., Vancouver- Robert Crumlin and Geoffrey Woad

Chris Johnson/Inge-Jean Mattson (UNBC)

Diavik Diamond Mines - Environment Department

EBA Engineering Consultants Ltd.

Gartner Lee Ltd.

Golder Associates Ltd.

Inmet Mining Corp.

Kelly Pennycook (Thebaché College)

Lutsel K'e Dene First Nation

Miramar Hope Bay Ltd.

Petr Cizek (consultant)

Rescan Environmental Services Ltd and BHP Billiton

Saskatchewan Environment

University of Alberta, Dept of Biological Sciences

Wolfden Resources

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SUBMITTED/IN REVIEW/IN PREPARATION:

- Cluff, H.D., P. C. Paquet, L. R. Walton and M. Musiani. 2010. Wolf ecology and management in the northern Canada. Perspectives from a snowmobile wolf hunt. Pages 235 – 259 in M. Musiani, L. Boitani, and P.C. Paquet, eds. The world of wolves: new perspectives on ecology, behavior and management . University of Calgary Press, Calgary, AB Canada.
- Frame, P.F., H.D. Cluff and D.S. Hik. (in review). Effects of prey availability and economic development on reproductive success of wolves. MS submitted to Ecology & Society.
- Hillis, T. 2008. *In prep.* Quality assessment of vegetation on the Bathurst caribou winter range at the landscape scale. Hillis, T. 2008. *In prep.* Snow accumulation and freeze/thaw patterns on the Bathurst caribou winter range: implications for detecting caribou movement patterns at the large scale.
- Hillis, T. 2008. *In prep.* Landscape scale attributes of caribou, *Rangifer tarandus caribou*, centers of activity on the Bathurst herd ranges.
- Mattson, I.-J., C.J. Johnson and H.D. Cluff. (submitted). Winter survey of Bathurst caribou and associated wolf distribution and abundance. Northwest Territories Department of Environment and Natural Resources Manuscript Report.
- Musiani, M., J.A. Leonard, H.D. Cluff, C.C. Gates, S. Mariani, P.C. Paquet, C. Vila', and R.K. Wayne. (submitted) Differentiation of tundra/taiga and boreal coniferous forest wolves: genetics, coat color and association with migratory caribou. MS submitted to Molecular Ecology.

PRESENTATIONS:

- Cluff, H.D., M. Musiani and P.C. Paquet. 2003. The NWT Rennie Lake area wolf kill: commercial hunt and predator control? Presentation given at the World Wolf Conference, Banff, AB, September 2003.
- Cluff, H.D. and I. Jonsen. 2006. Movement patterns of wolves on extended trips on the tundra. Presentation given at the Wildlife and Environmental Impact Assessment Conference, Yellowknife, NT, March 2006.
- Hillis, T. 2008. Using snow characteristics to detect caribou movement patterns within the Bathurst caribou winter range.
- Musiani, M., C.C. Gates, P.C. Paquet, H.D. Cluff, L.R Walton, P.J. Wilson and B.N. White. 2001. Hunting, migration and sinks/sources among Northern Canadian wolf populations. Canid Biology and Conservation International Conference, Oxford, UK, September 2001.

APPENDIX C: Contract Report 2002: Turning angle and displacement of satellite collared caribou using correlated random walk models and fractal analysis

John Boulanger and Anne Gunn

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.

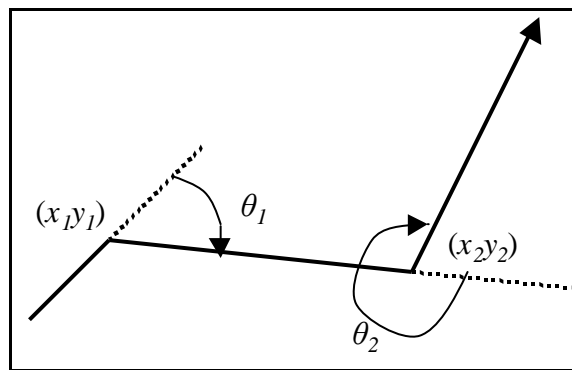


Figure 1. Parameterization of turning angles (θ) relative to successive GPS locations $(x_1, y_1$ and $x_2, y_2)$.

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 Raliegths 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

Predicted (CRW) variance	Observed 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.

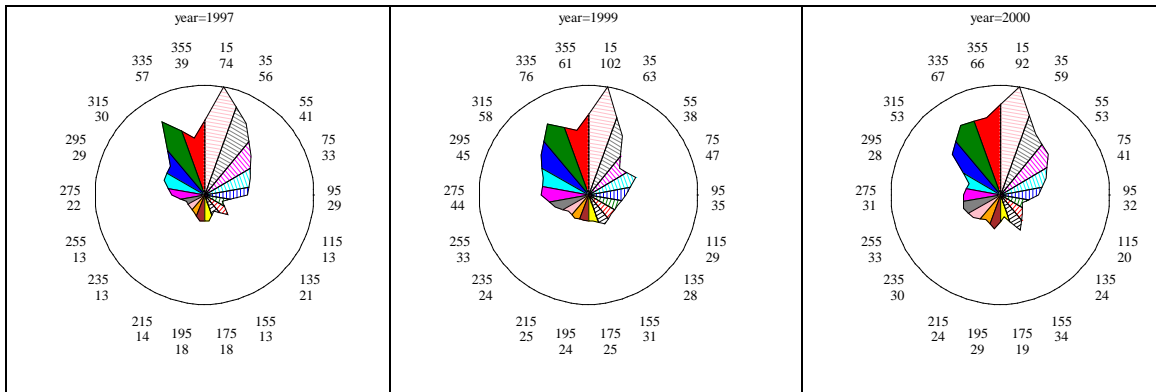


Figure 2. Pooled turning angles for each year of the analysis.

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.

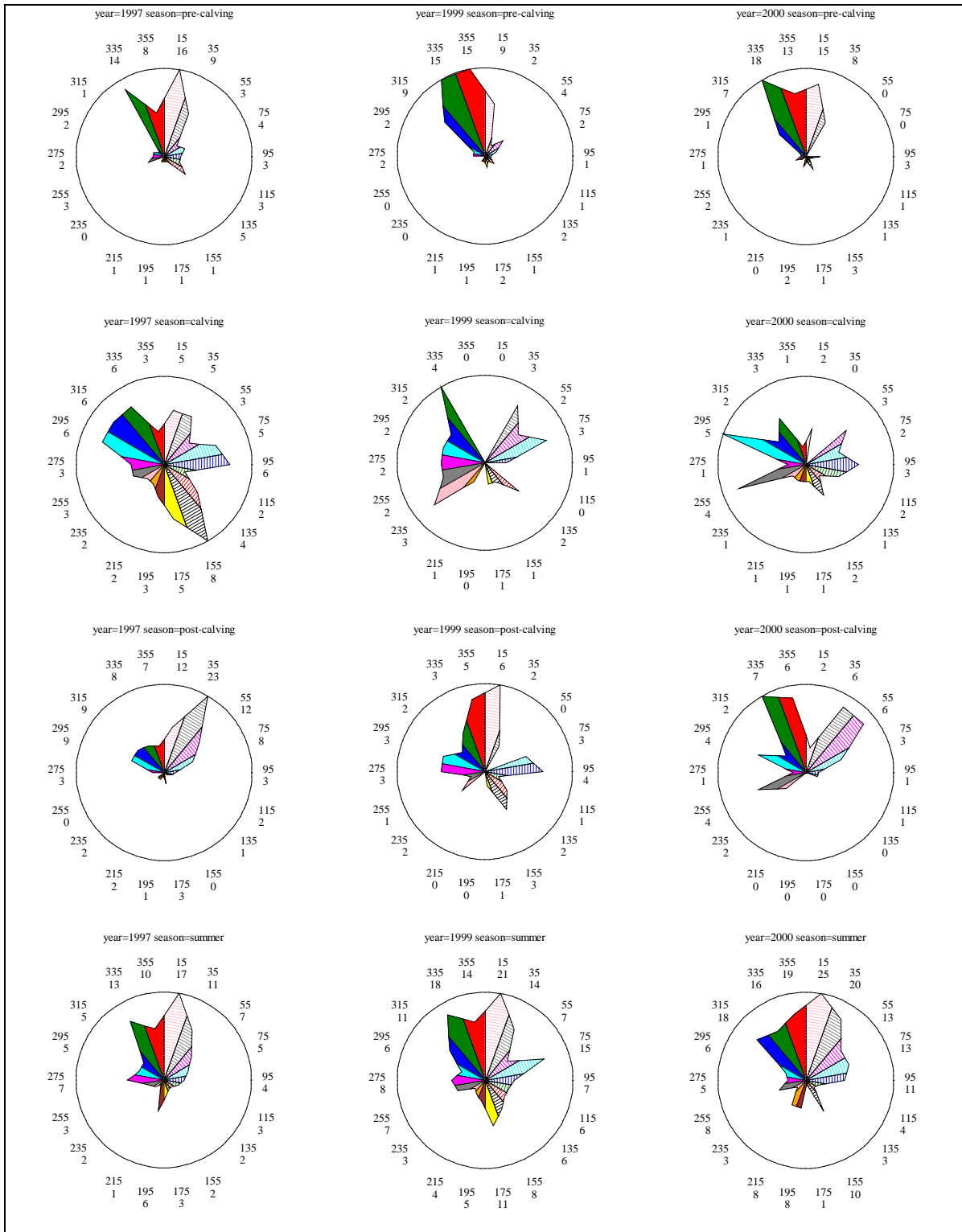


Figure 3. Distributions of turning angles by year and season (continued on next page)

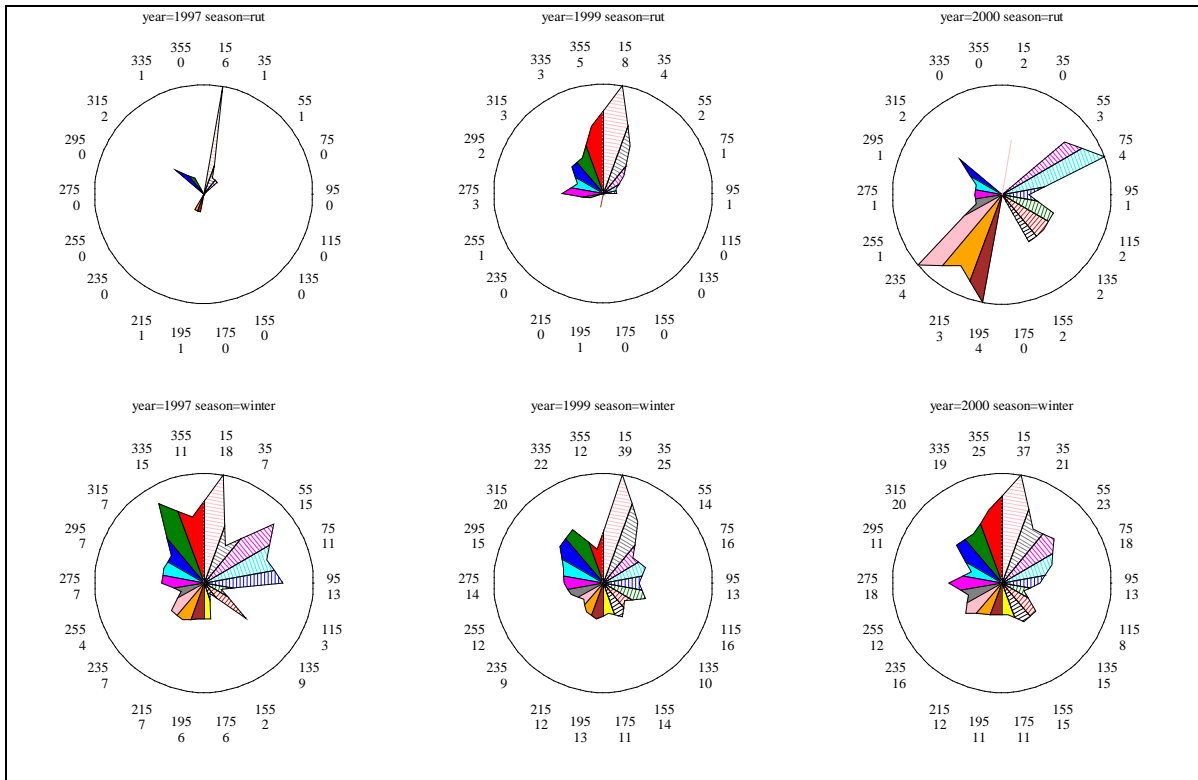


Figure 3 (continued). Distributions of turning angles by year and season

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.

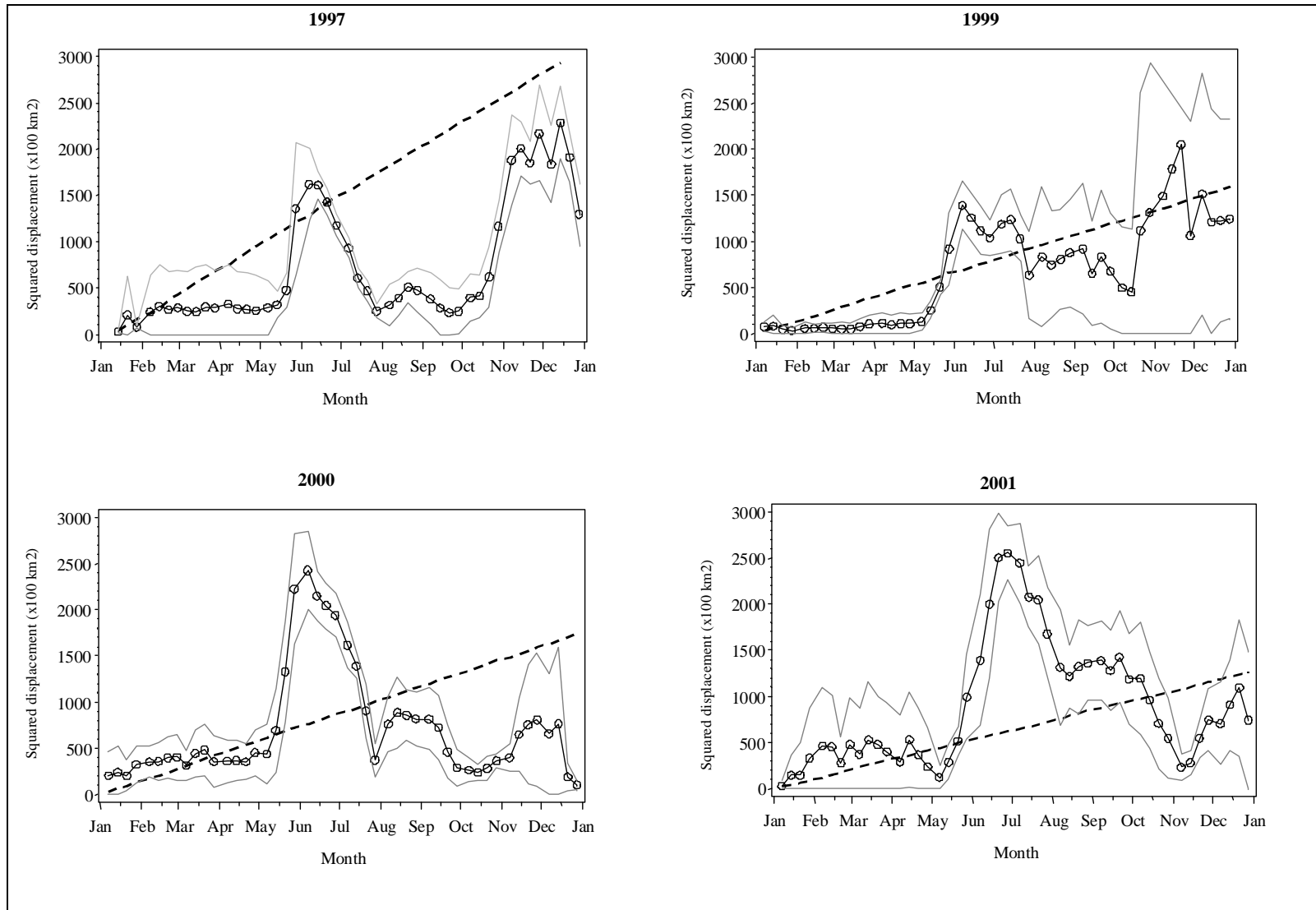


Figure 4. Annual observed and predicted displacements

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.

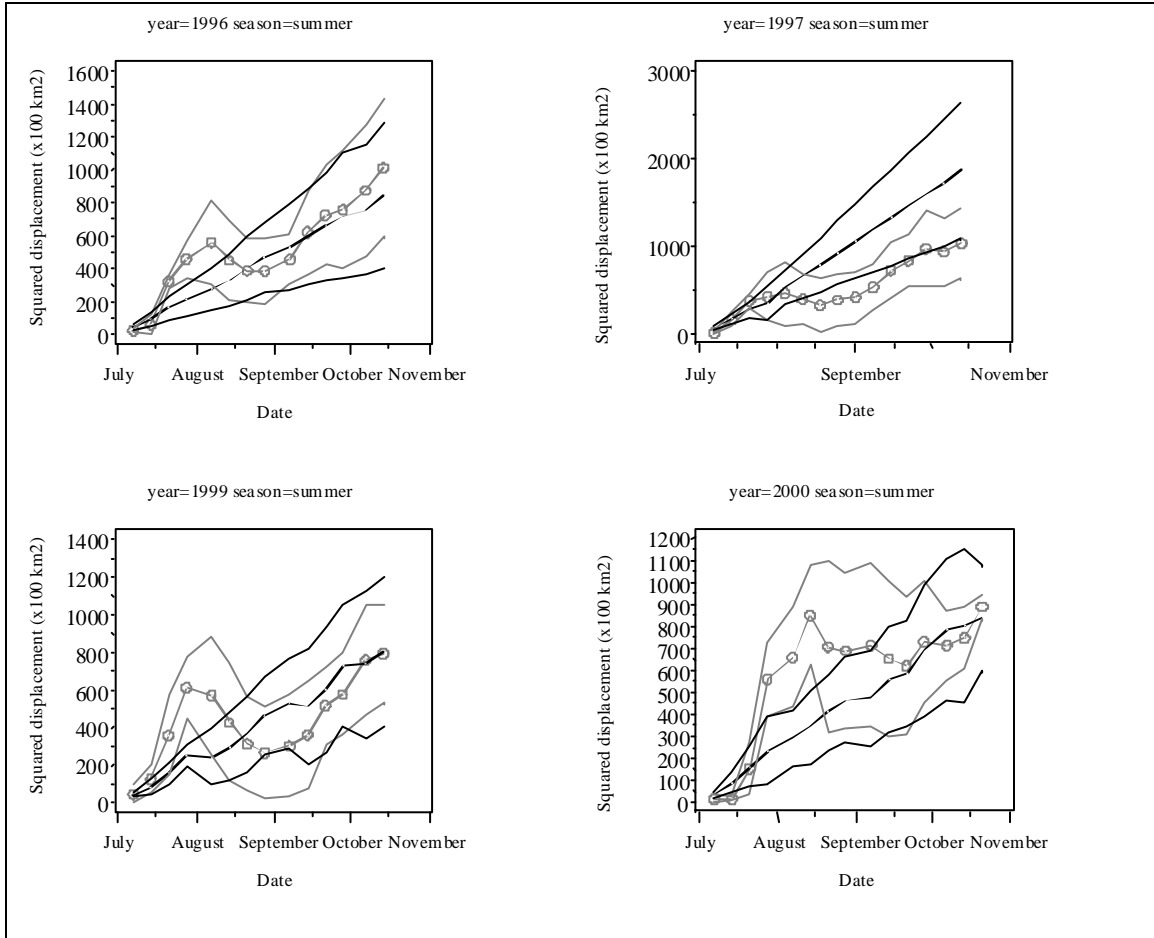


Figure 5. Observed and predicted displacement for the summer season. Solid black line shows correlated random walk predictions and associated standard deviation. Grey lines show observed displacement.

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.

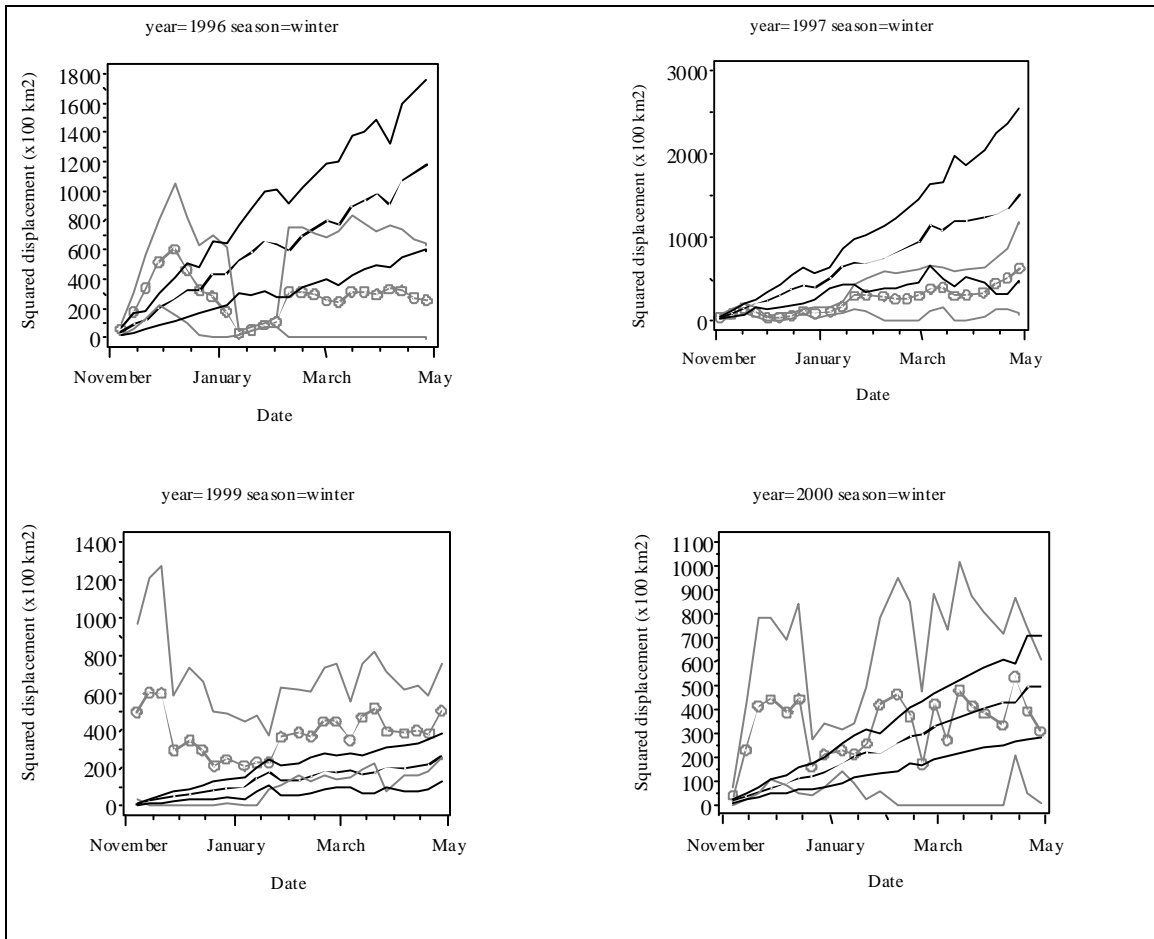


Figure 6. Observed and predicted displacement for the winter season

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.

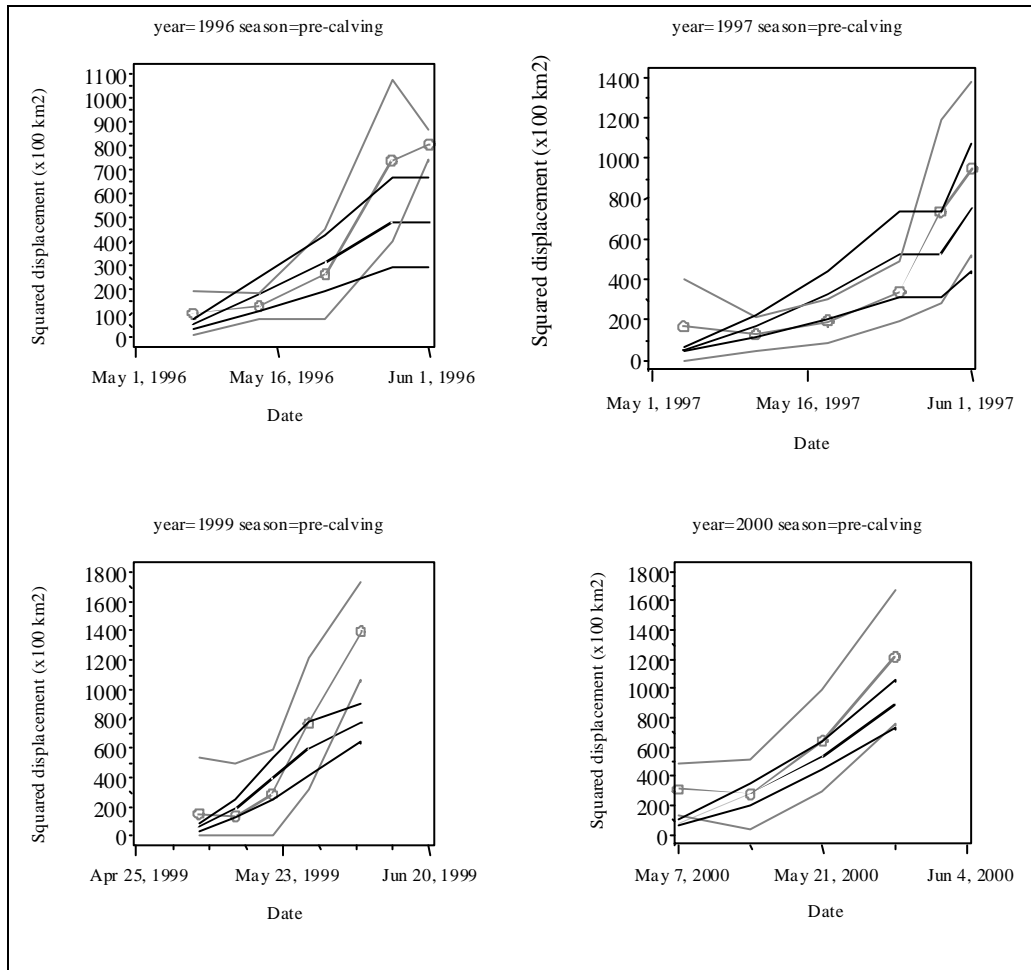


Figure 7. Observed and predicted displacement for the pre-calving season

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.

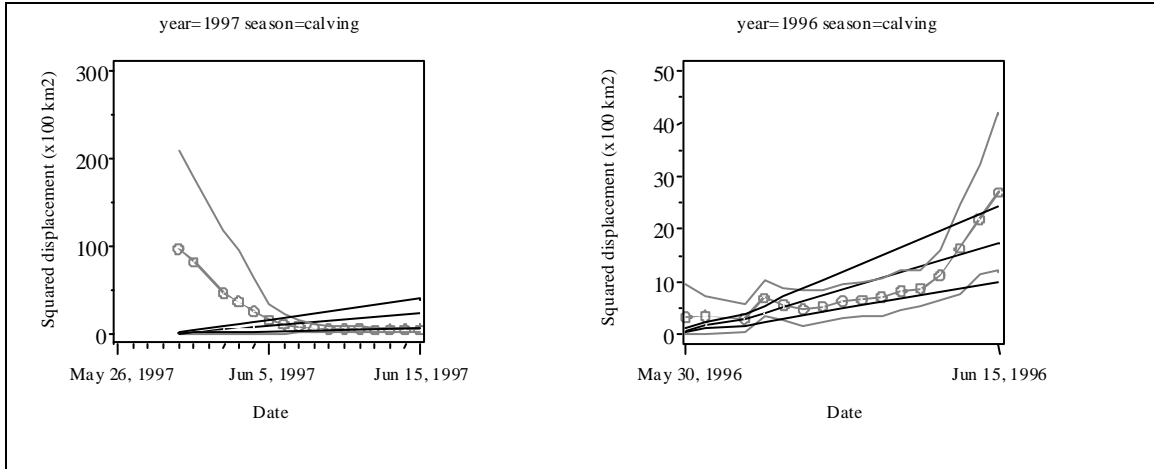


Figure 8. Observed and predicted displacement for the calving season

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.

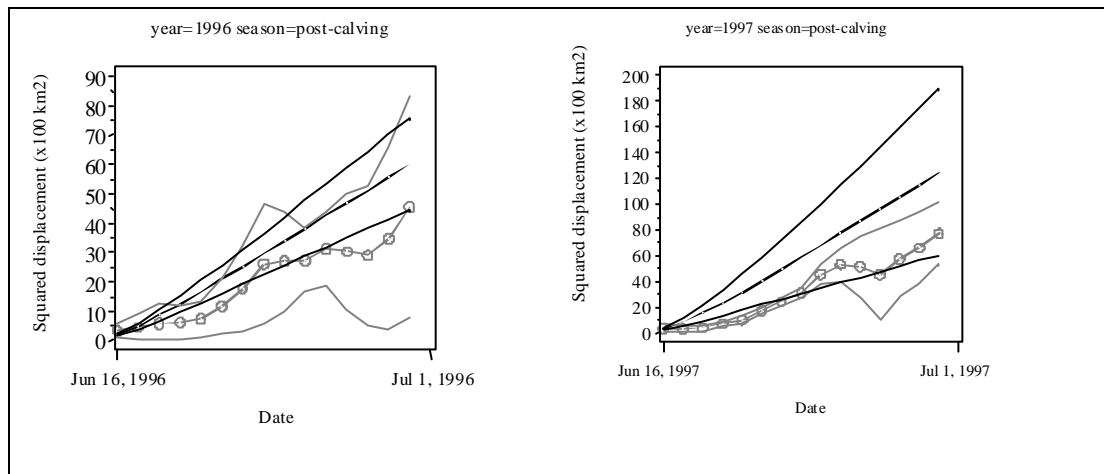


Figure 9. Observed and predicted displacement for the post-calving season

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
<i>Analysis 1-seasonal differences</i>			
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
<i>Analysis 2-yearly differences</i>			
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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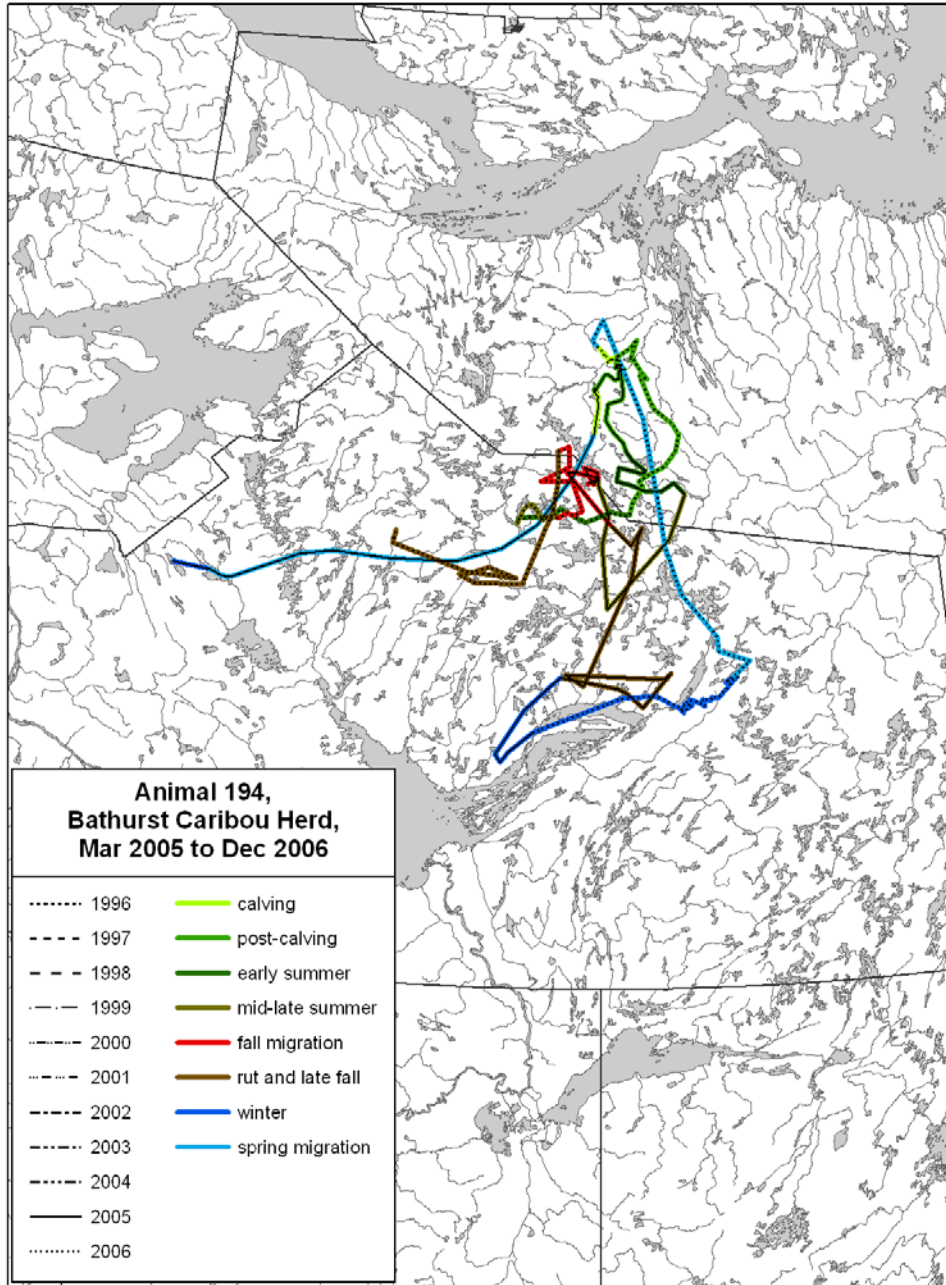
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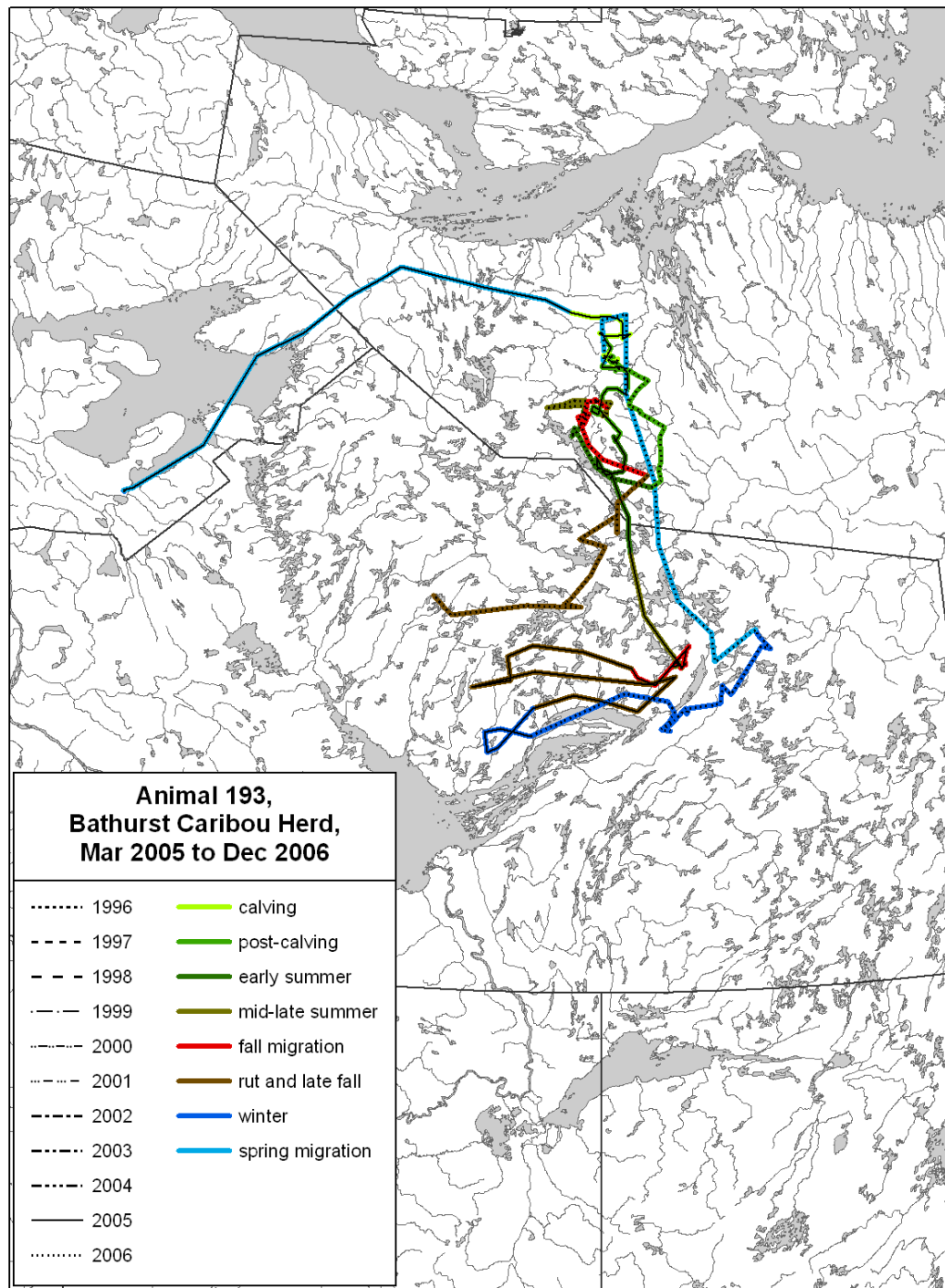
APPENDIX 1: Autocorrelation estimates for distances moved

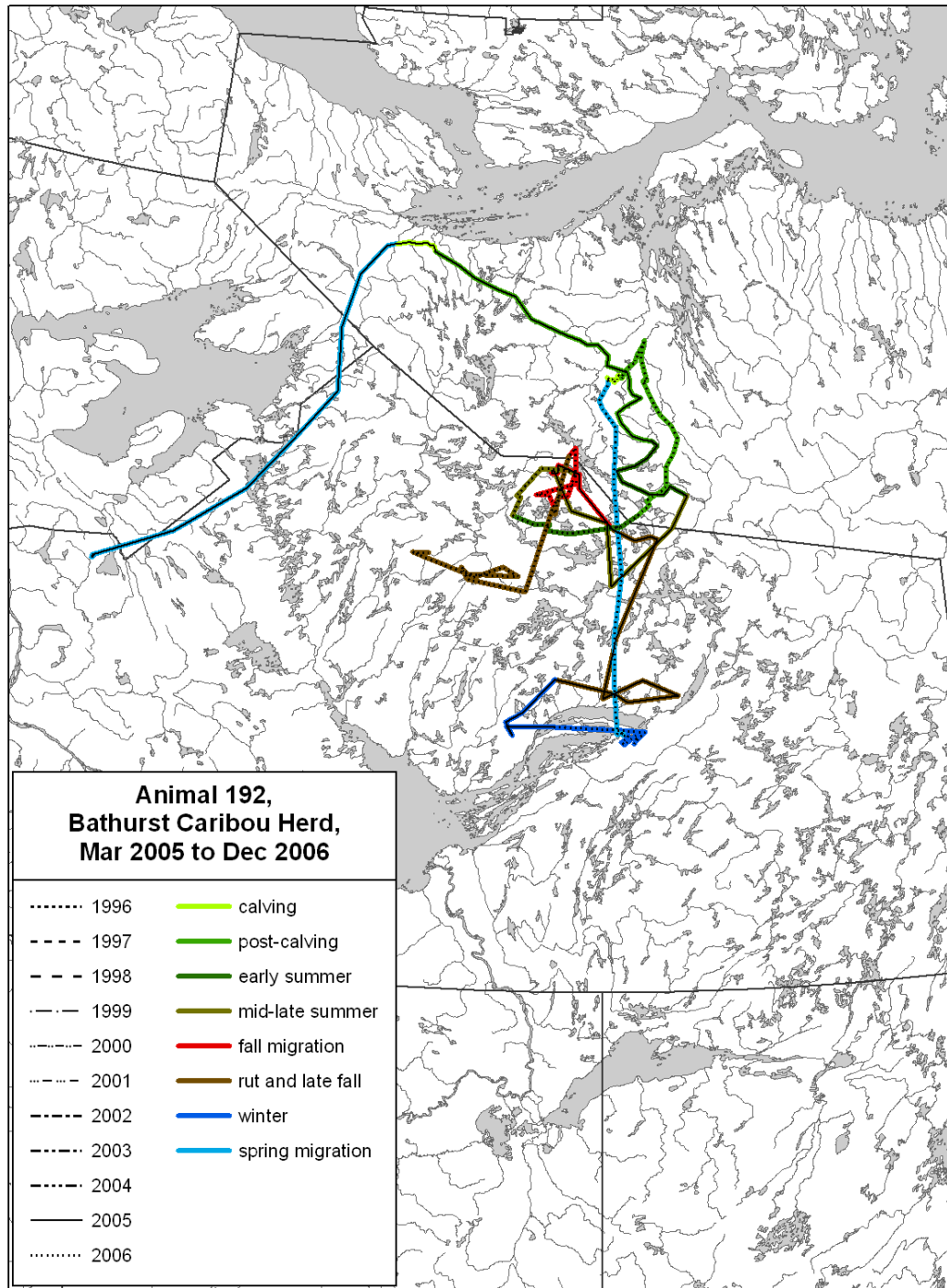
Season	Year	Autocorrelation estimates at successive time lags ¹										n
		1		2		3		4		5		
		\bar{x}	\bar{s}	\bar{x}	\bar{s}	\bar{x}	\bar{s}	\bar{x}	\bar{s}	\bar{x}	\bar{s}	
calving	1996	<i>0.34</i>	0.05	<i>0.15</i>	0.07	-0.02	0.04	-0.13	0.02	-0.18	0.05	9
	1997	0.22	0.11	-0.04	0.13	-0.08	0.07	-0.11	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	<i>0.04</i>	-0.08	0.04	0.00	0.03	-0.04	0.04	7
	1999	<i>0.13</i>	0.04	-0.05	0.06	-0.03	0.05	-0.02	0.05	-0.05	0.04	16

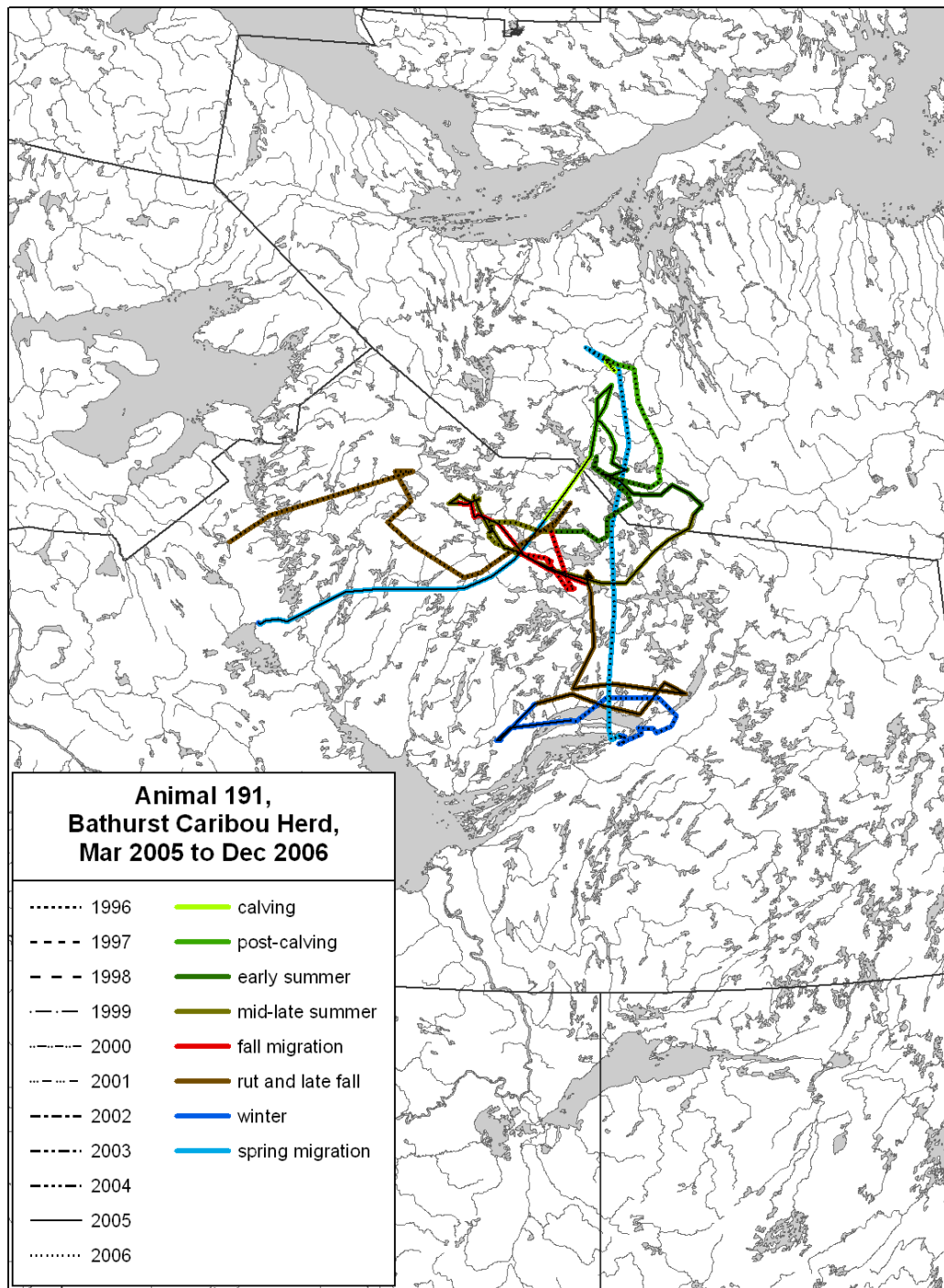
¹Estimates in *italics* were significantly different than 0 at an α level of 0.05.

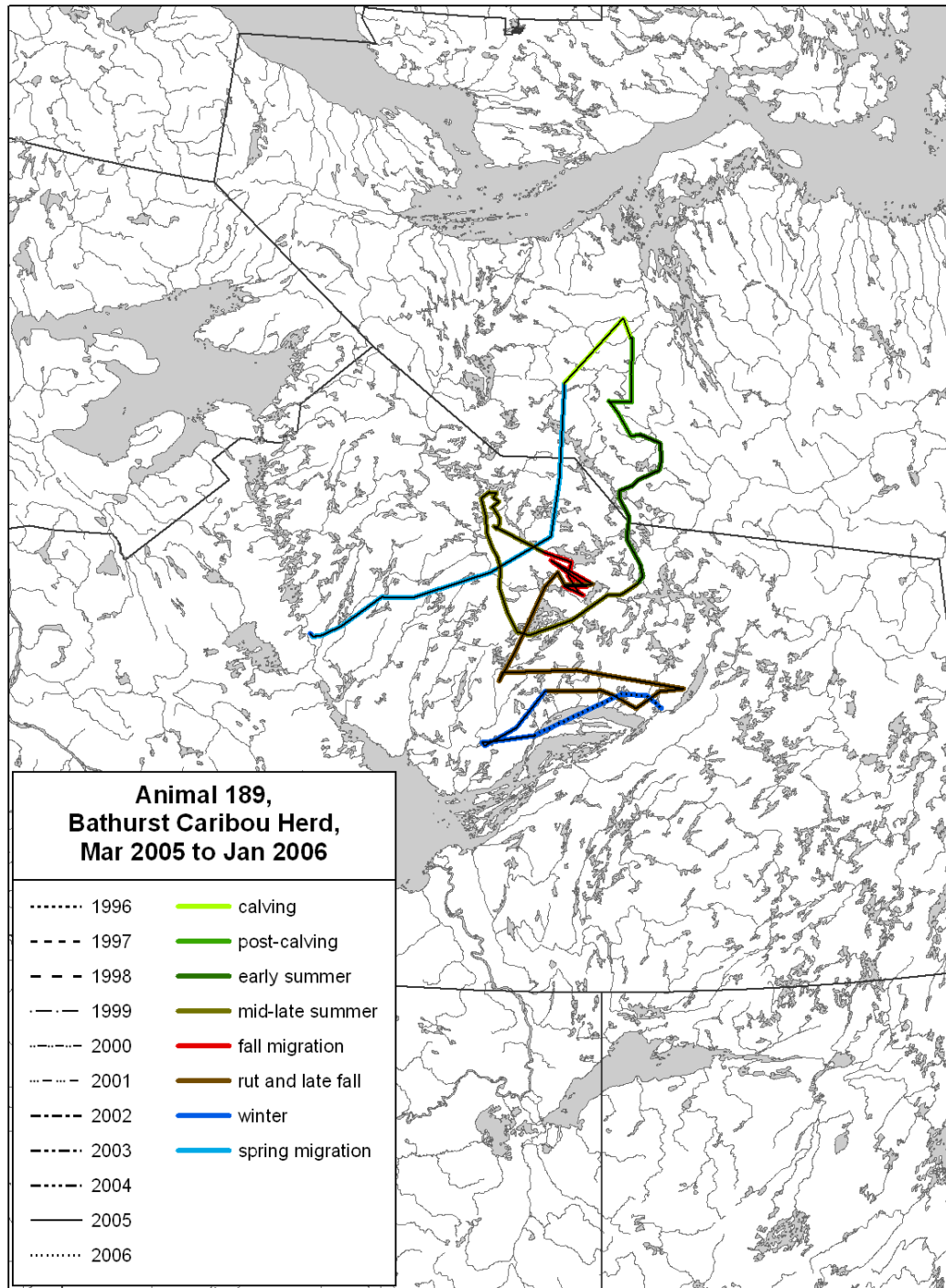
APPENDIX D: Individual tracks for each satellite collared cow, Bathurst herd

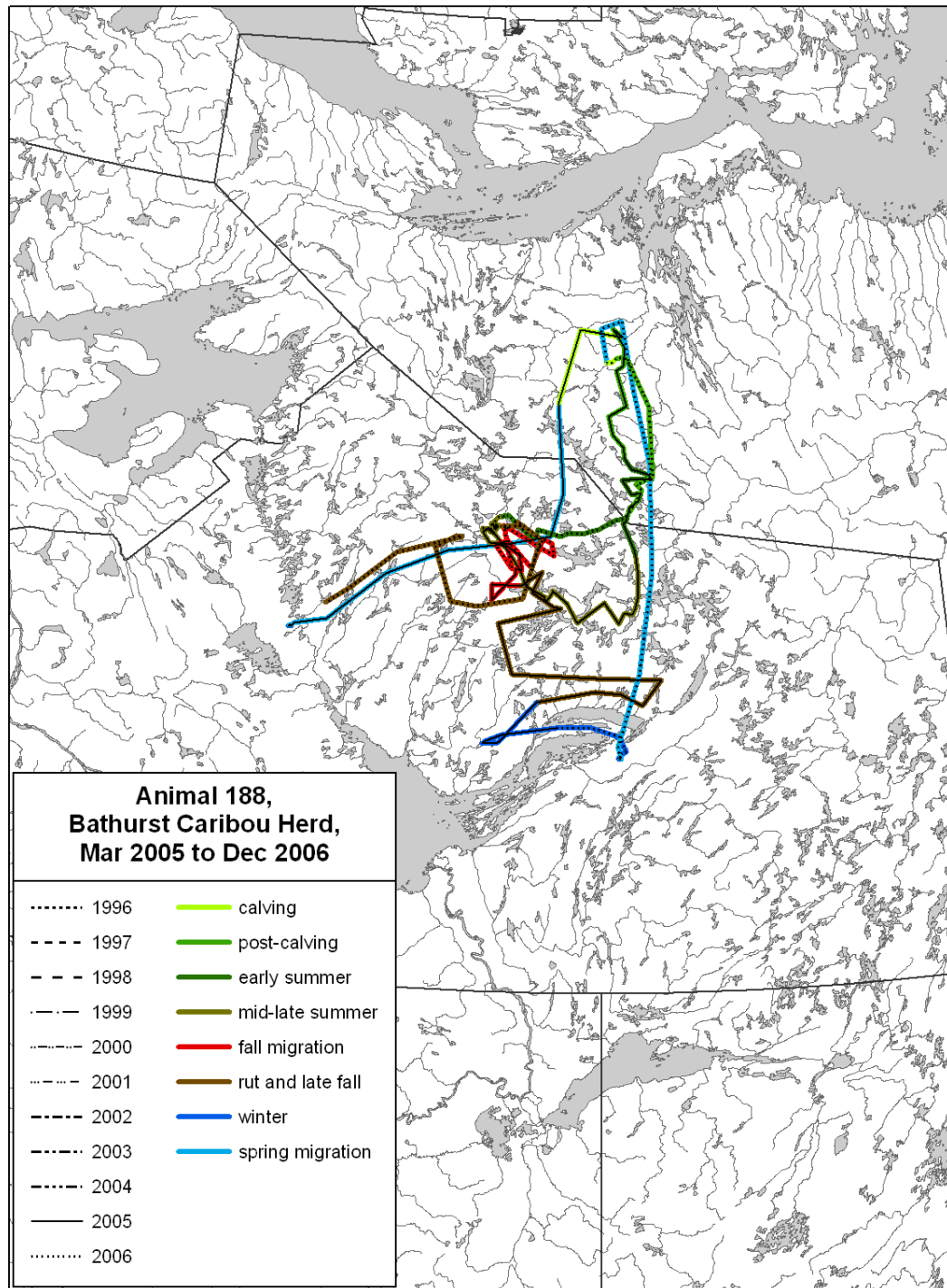


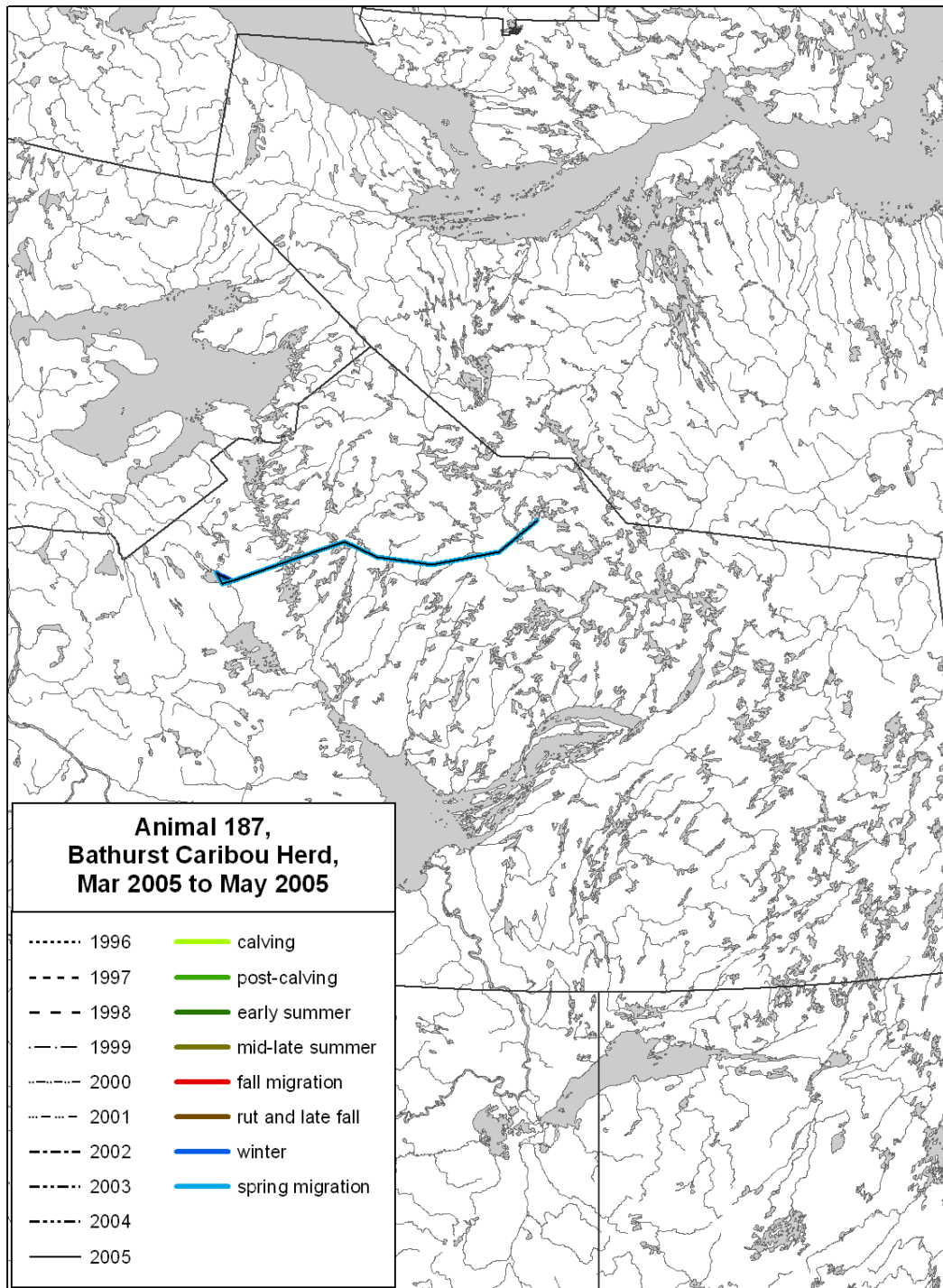


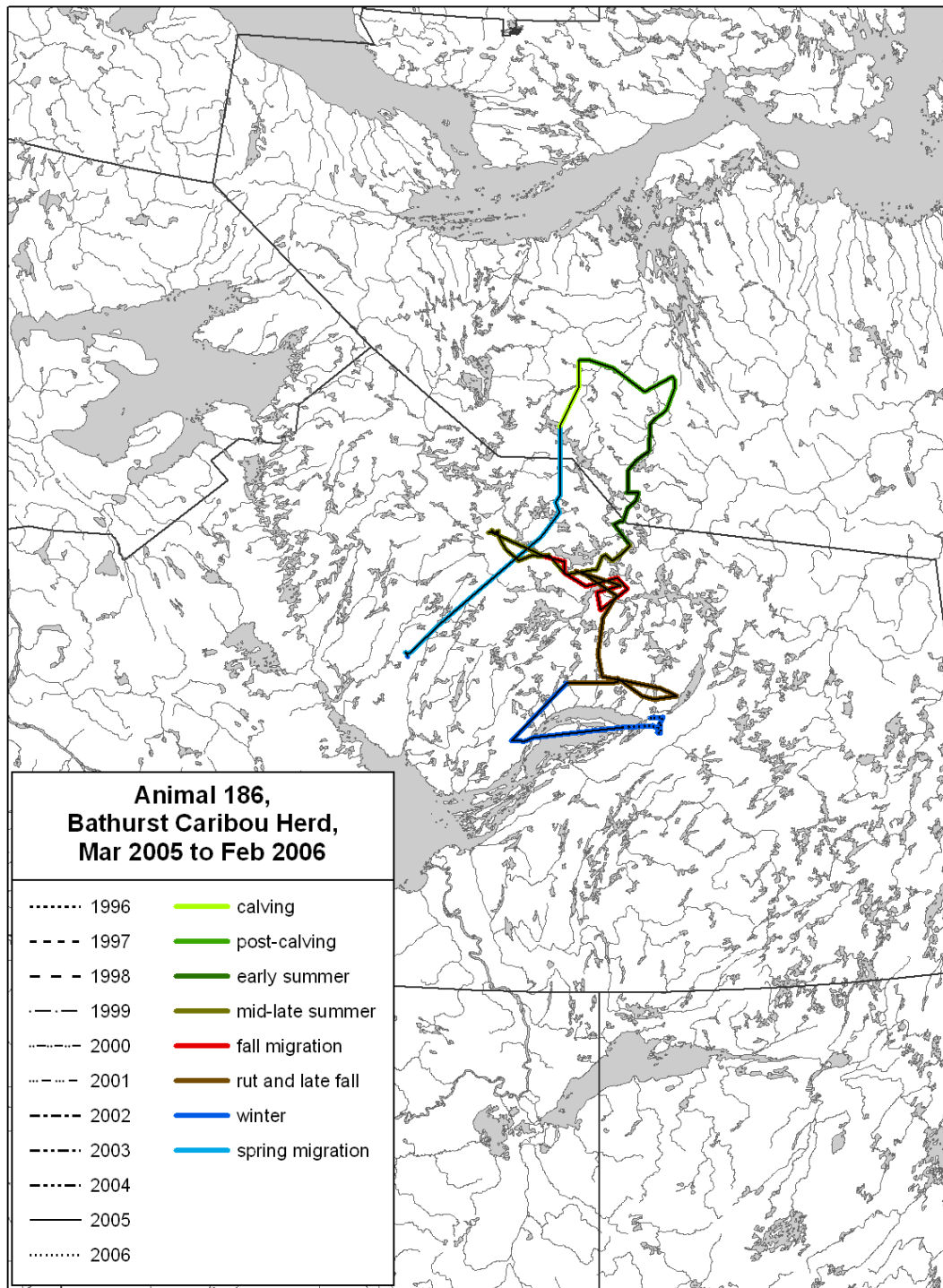


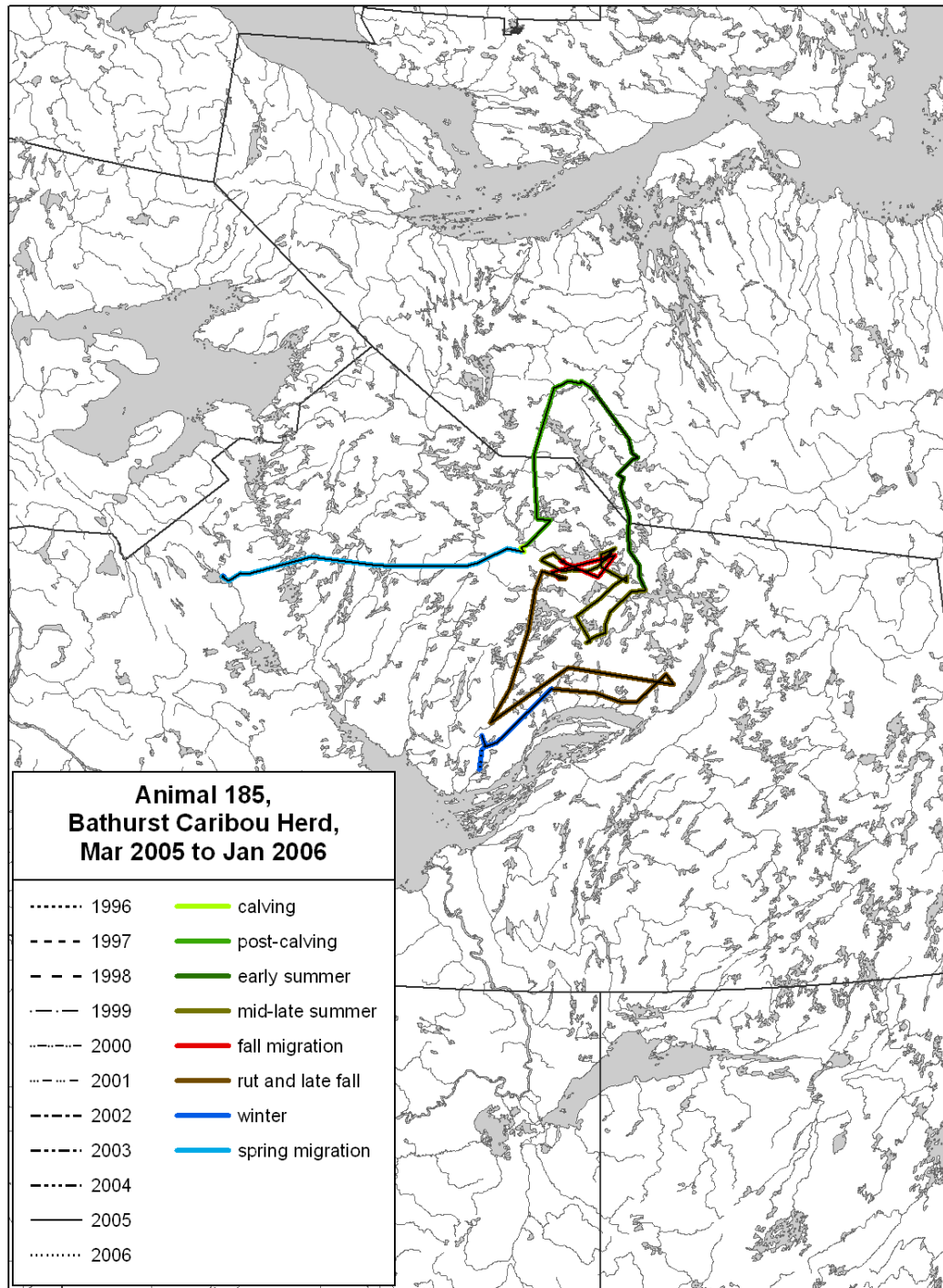


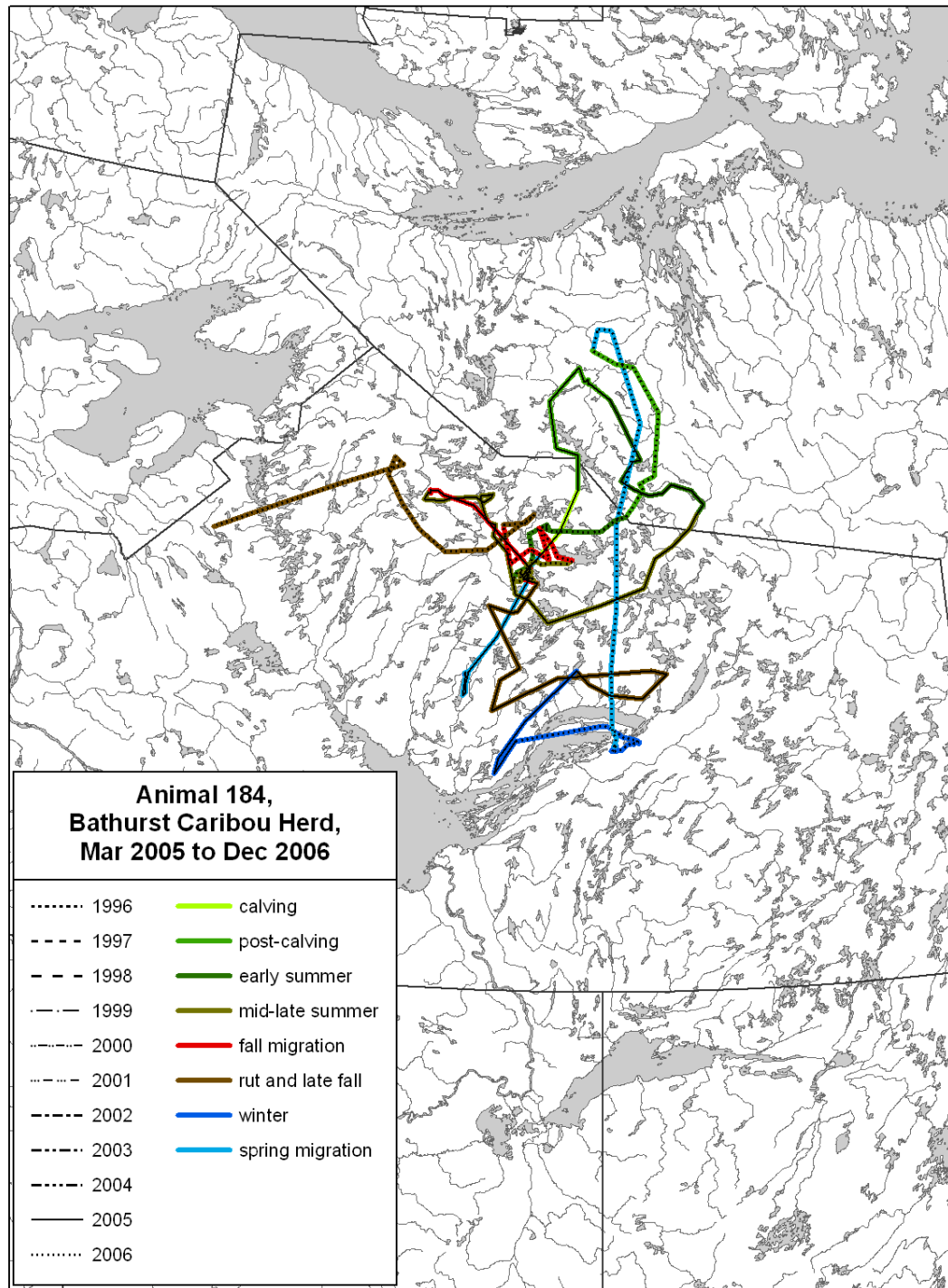


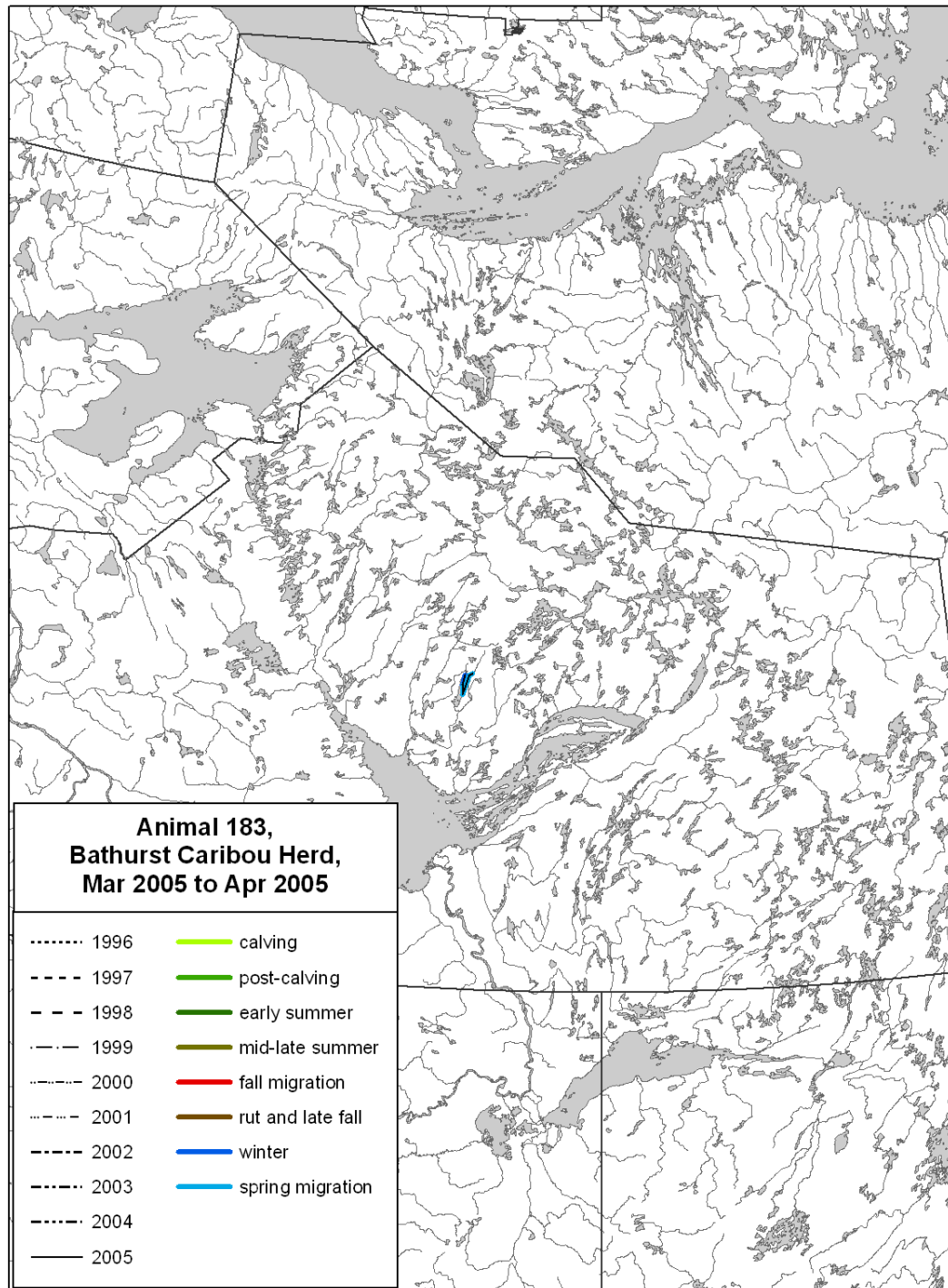


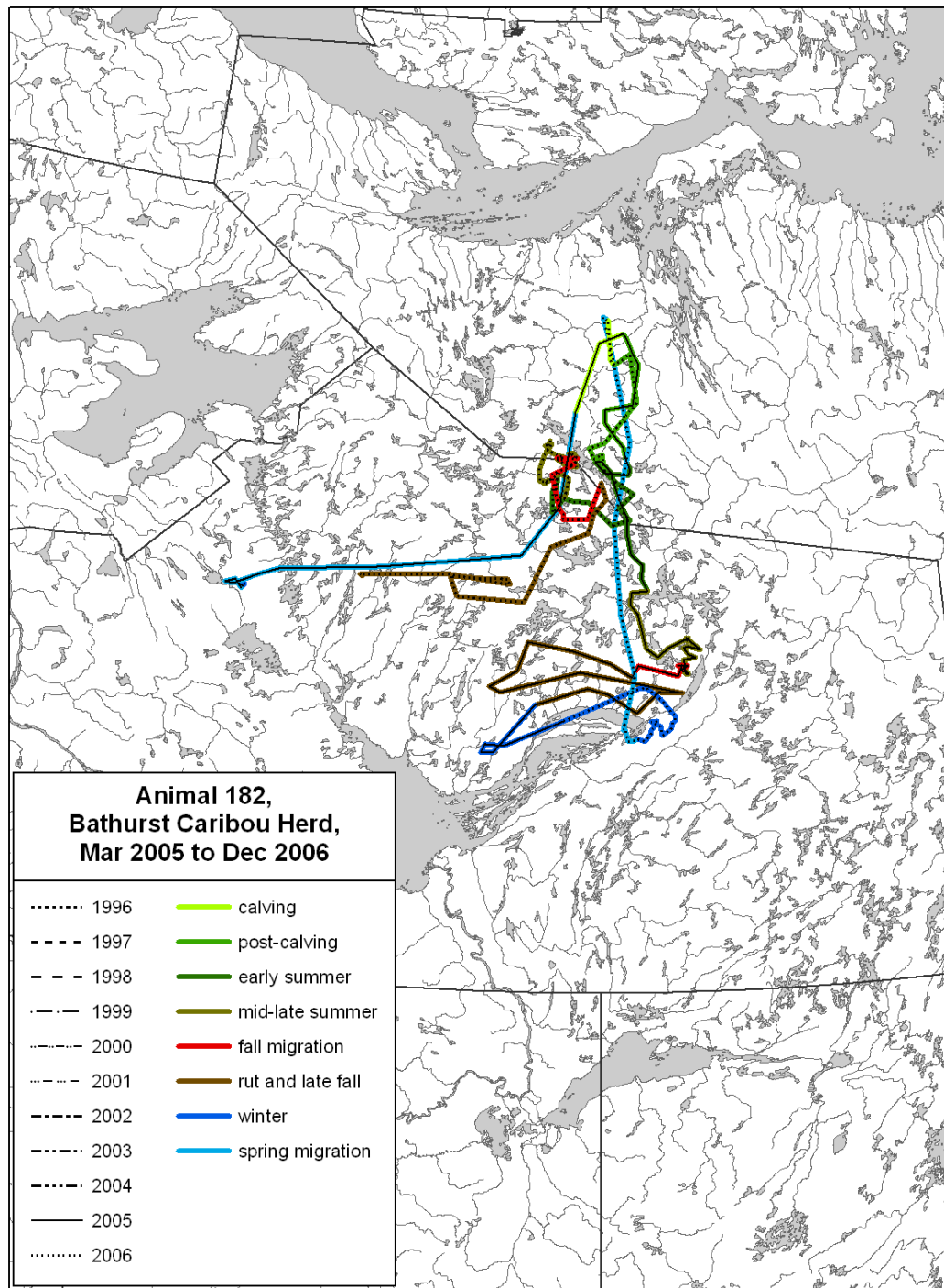


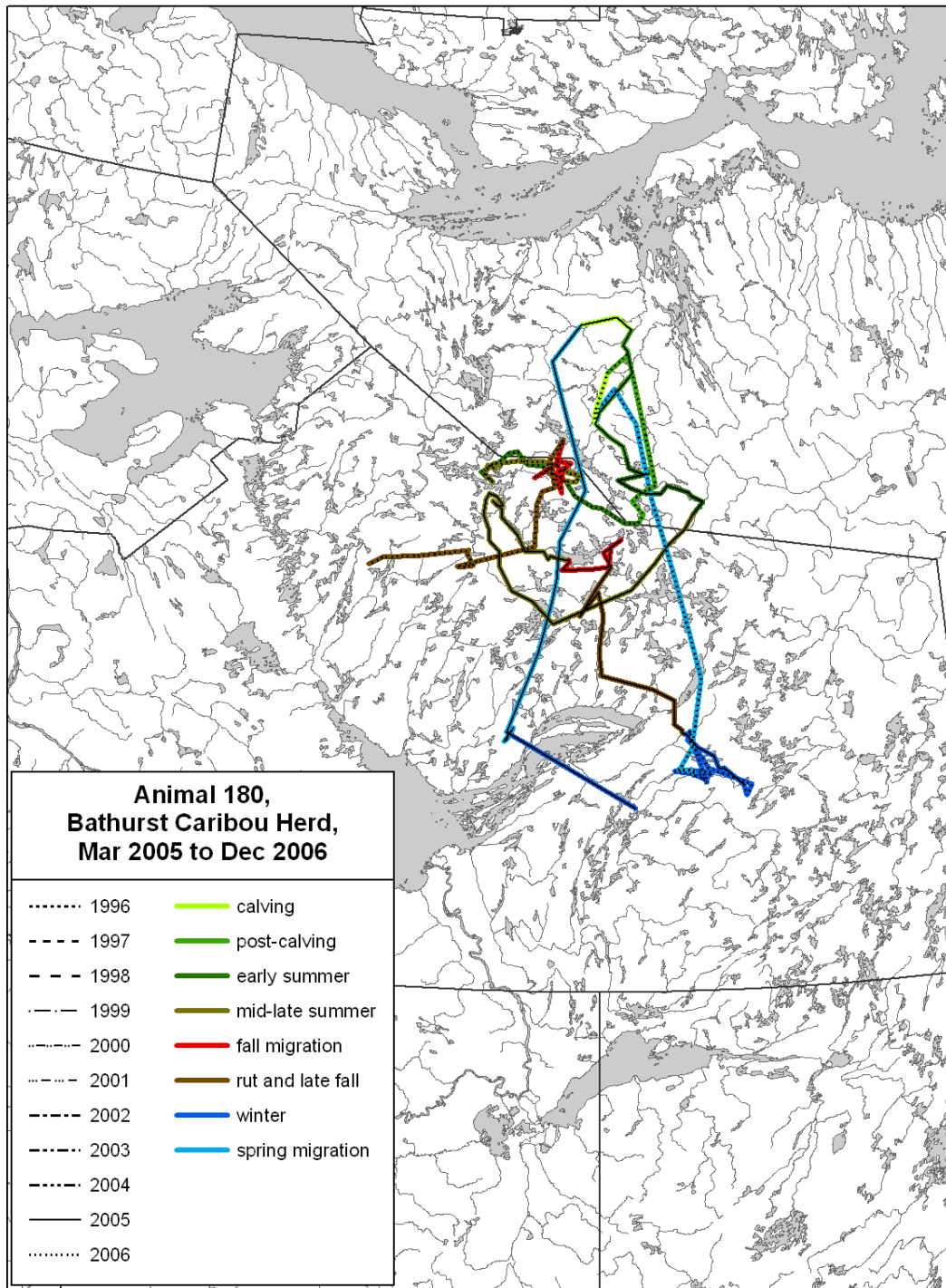


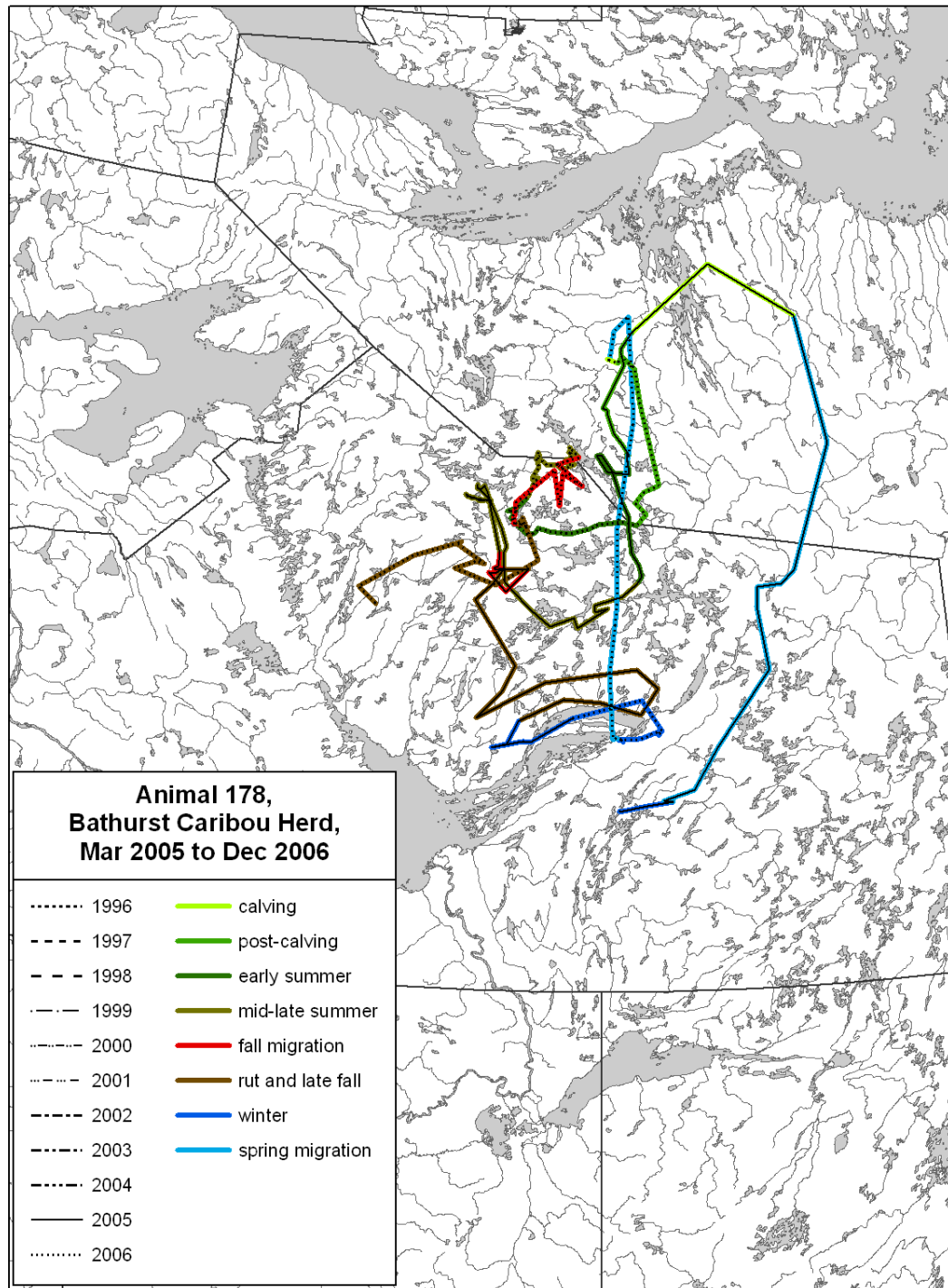


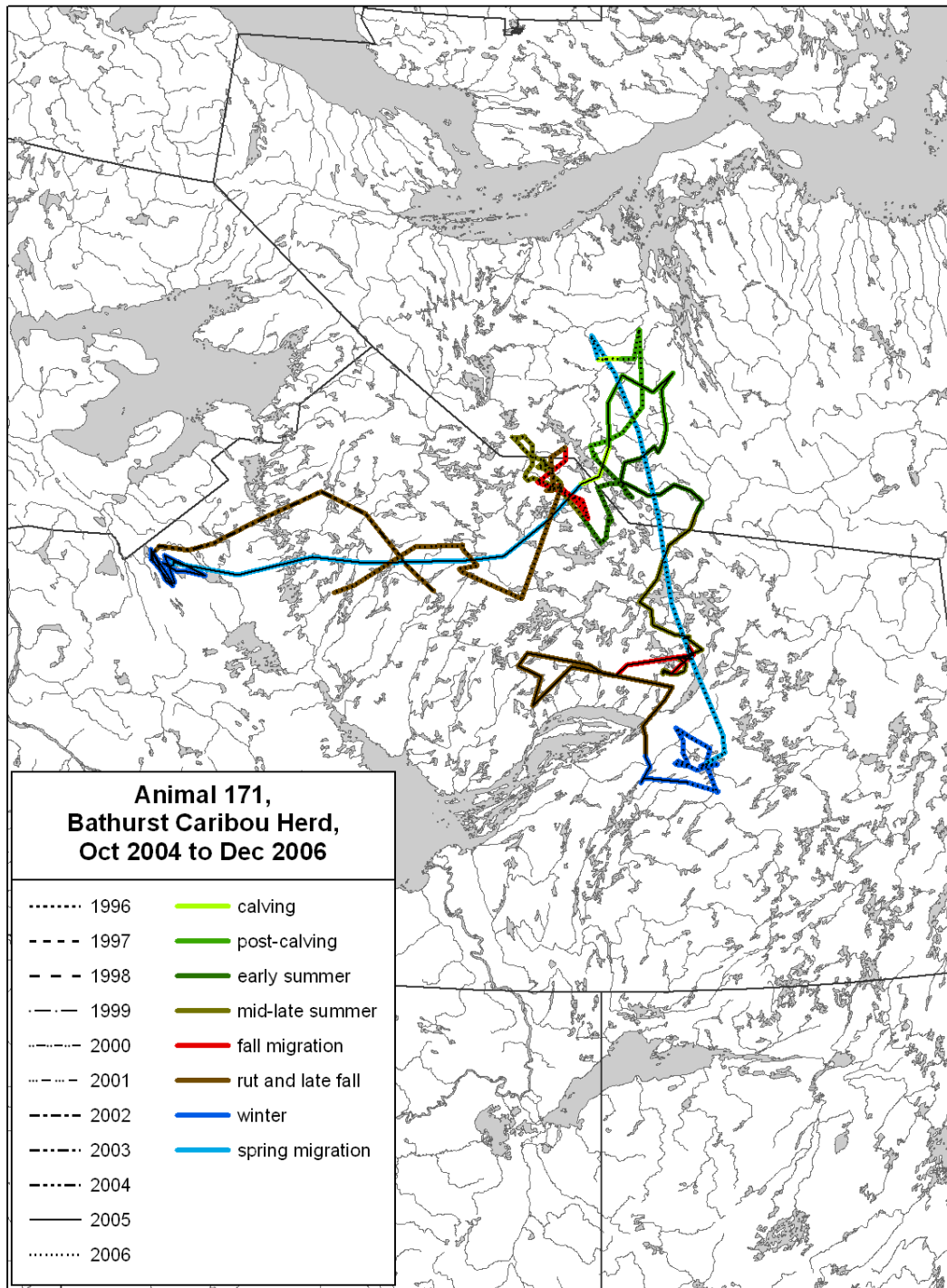


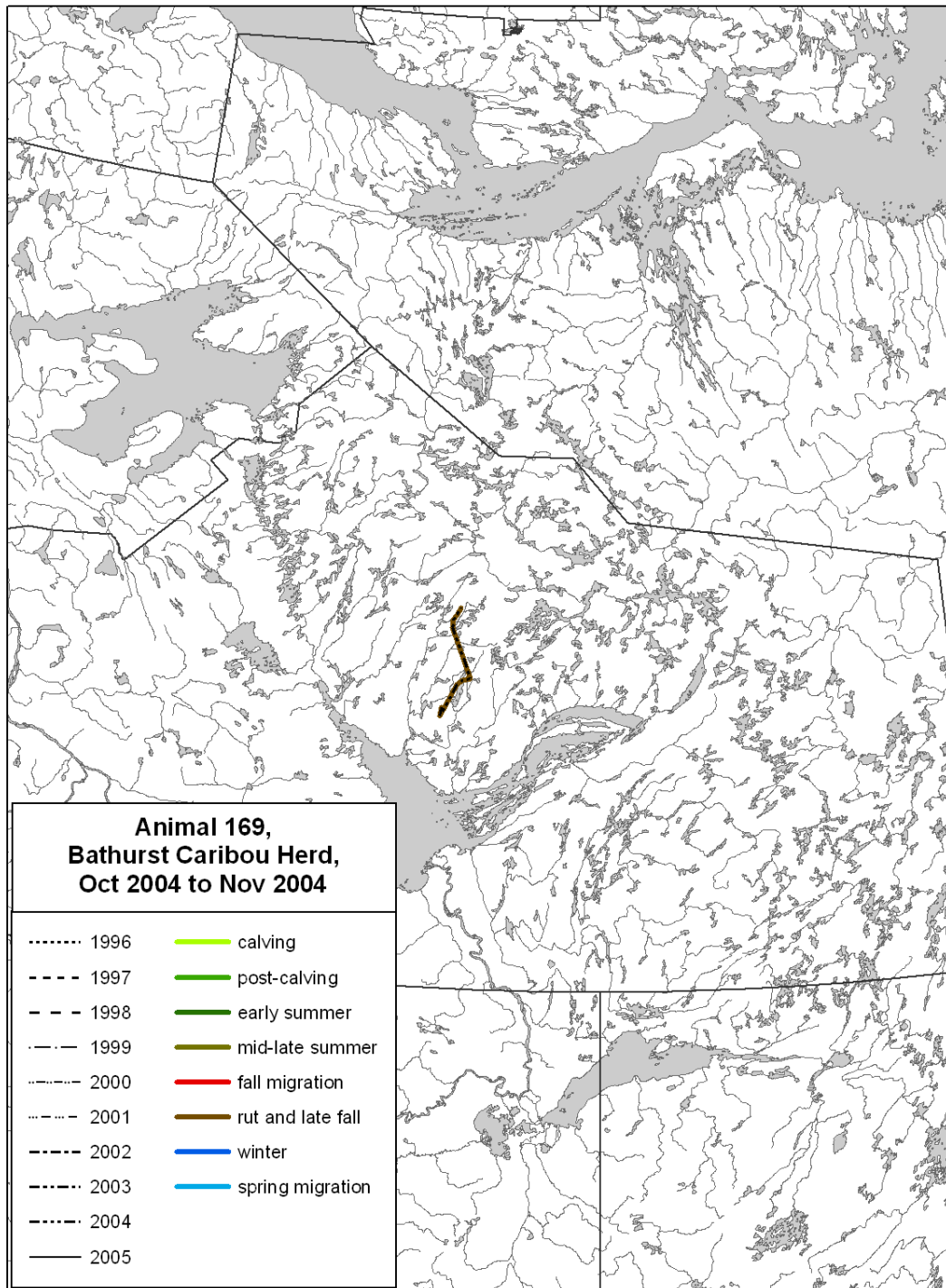


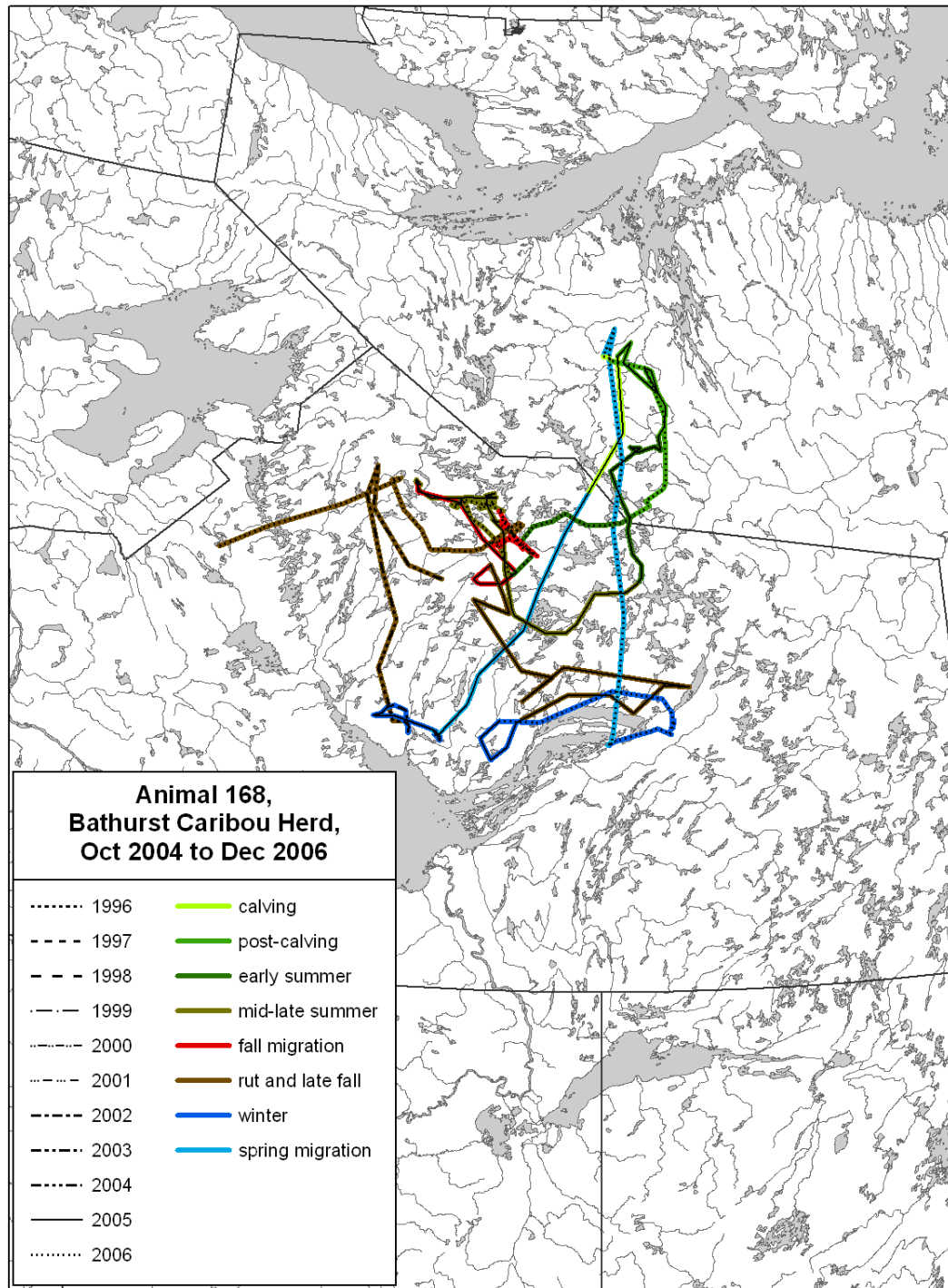


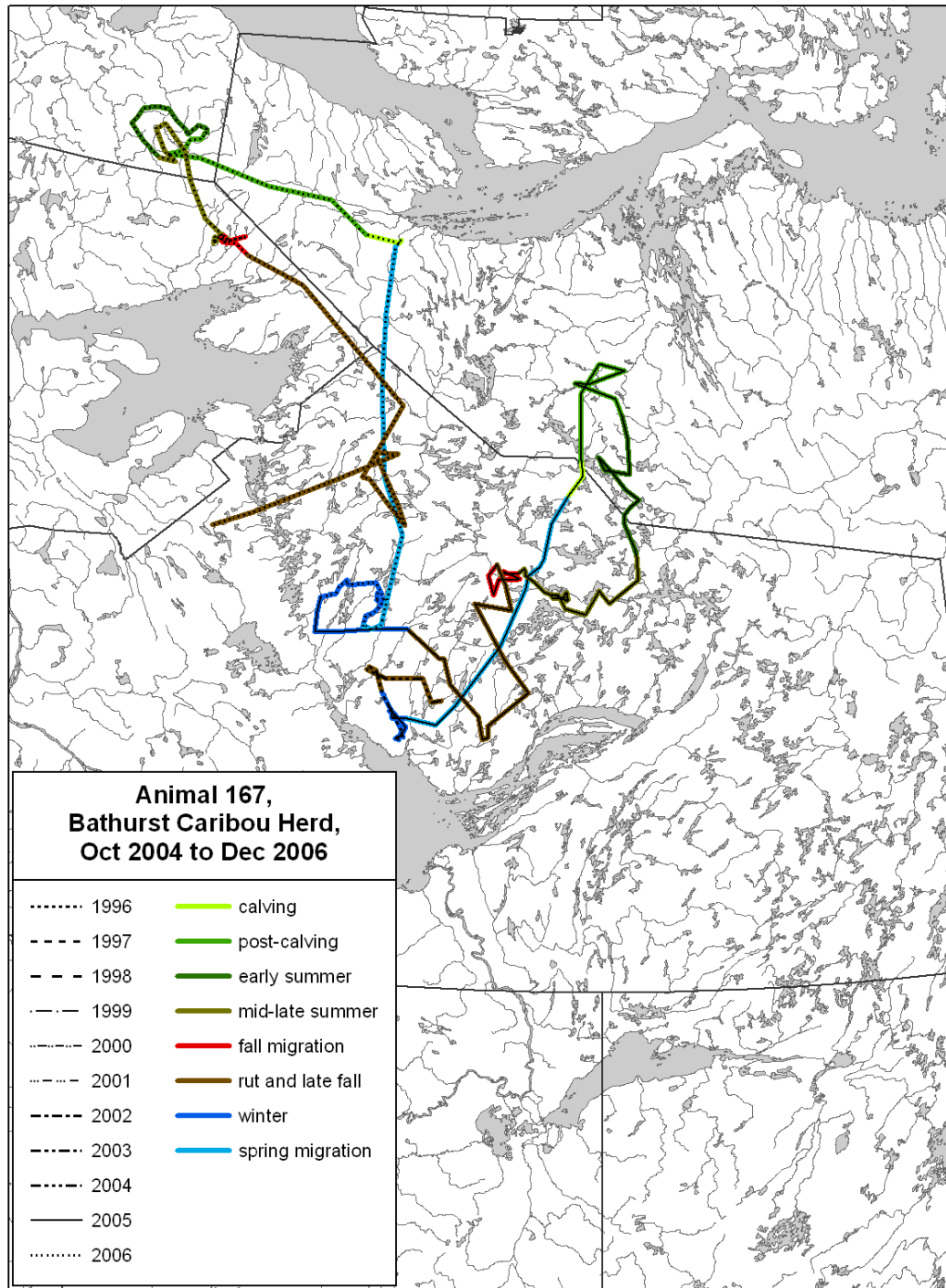


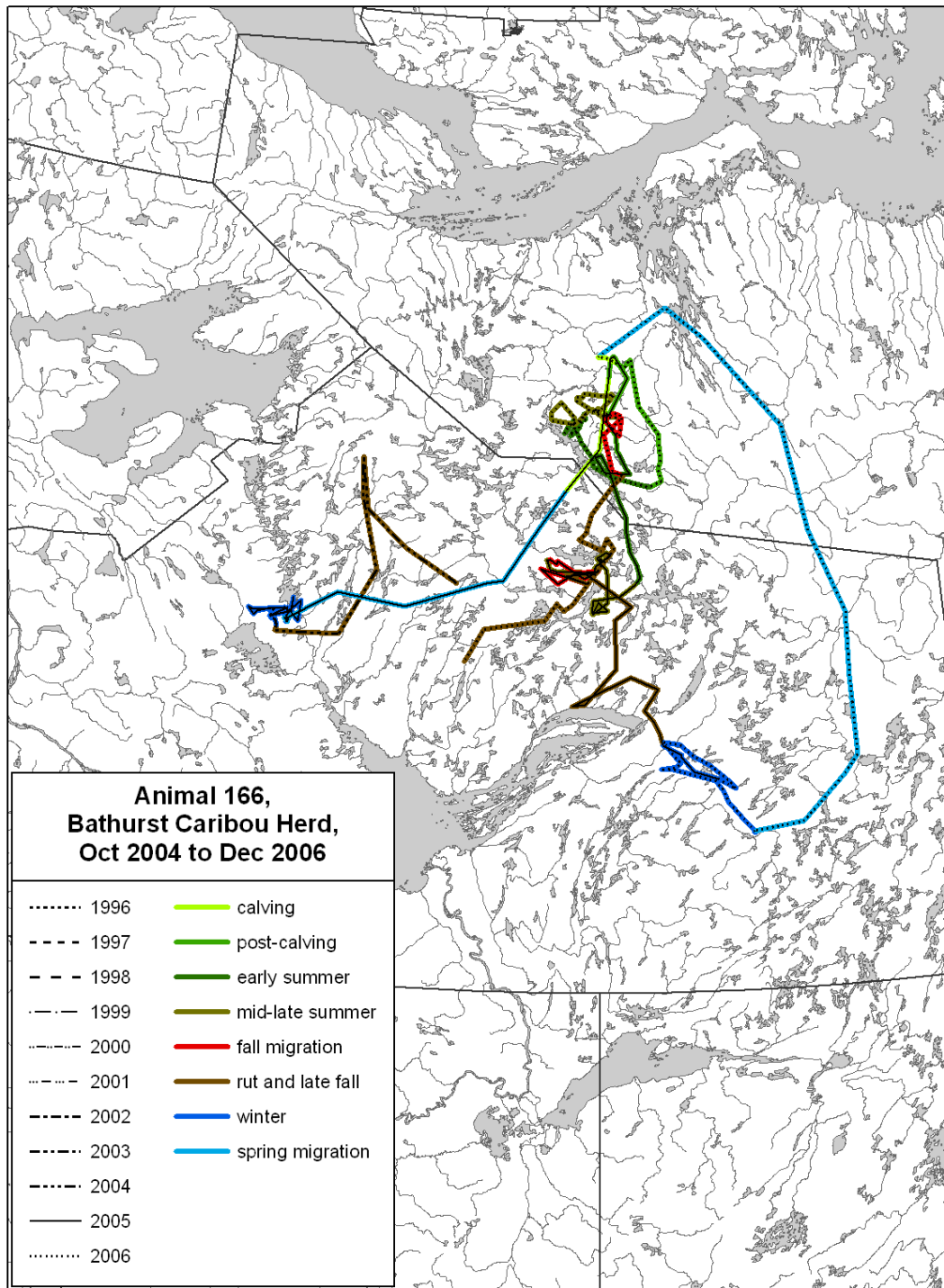


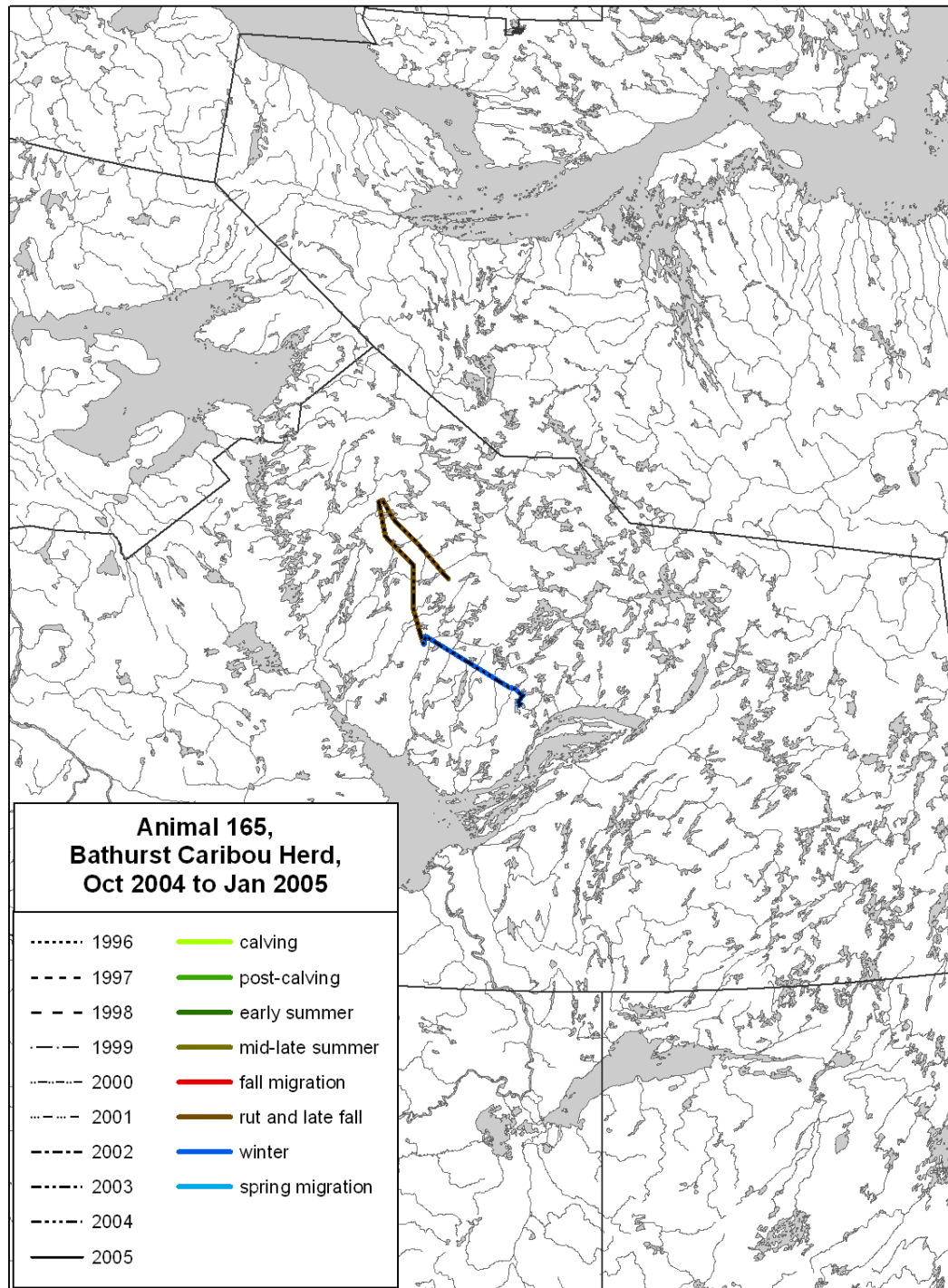


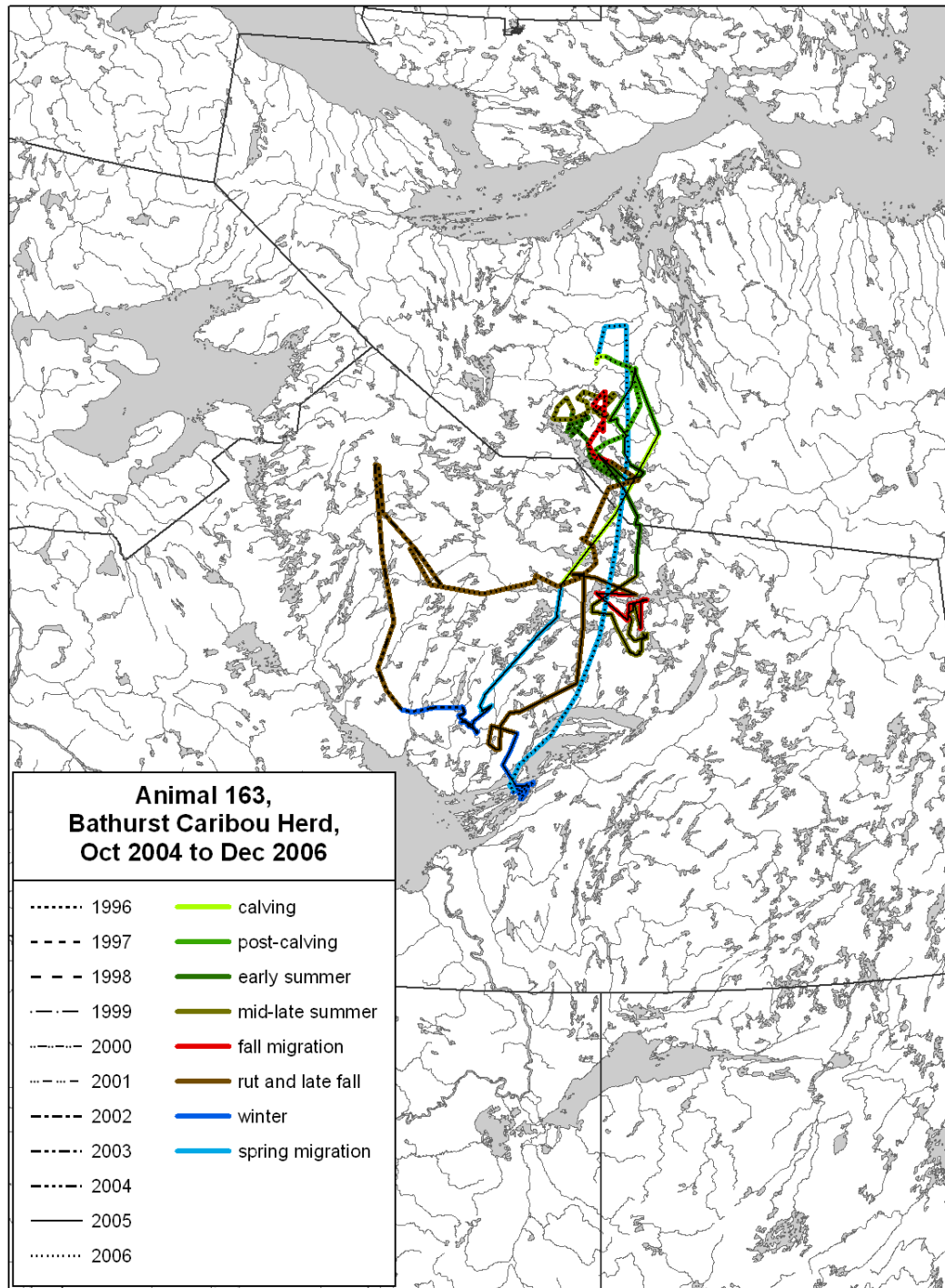


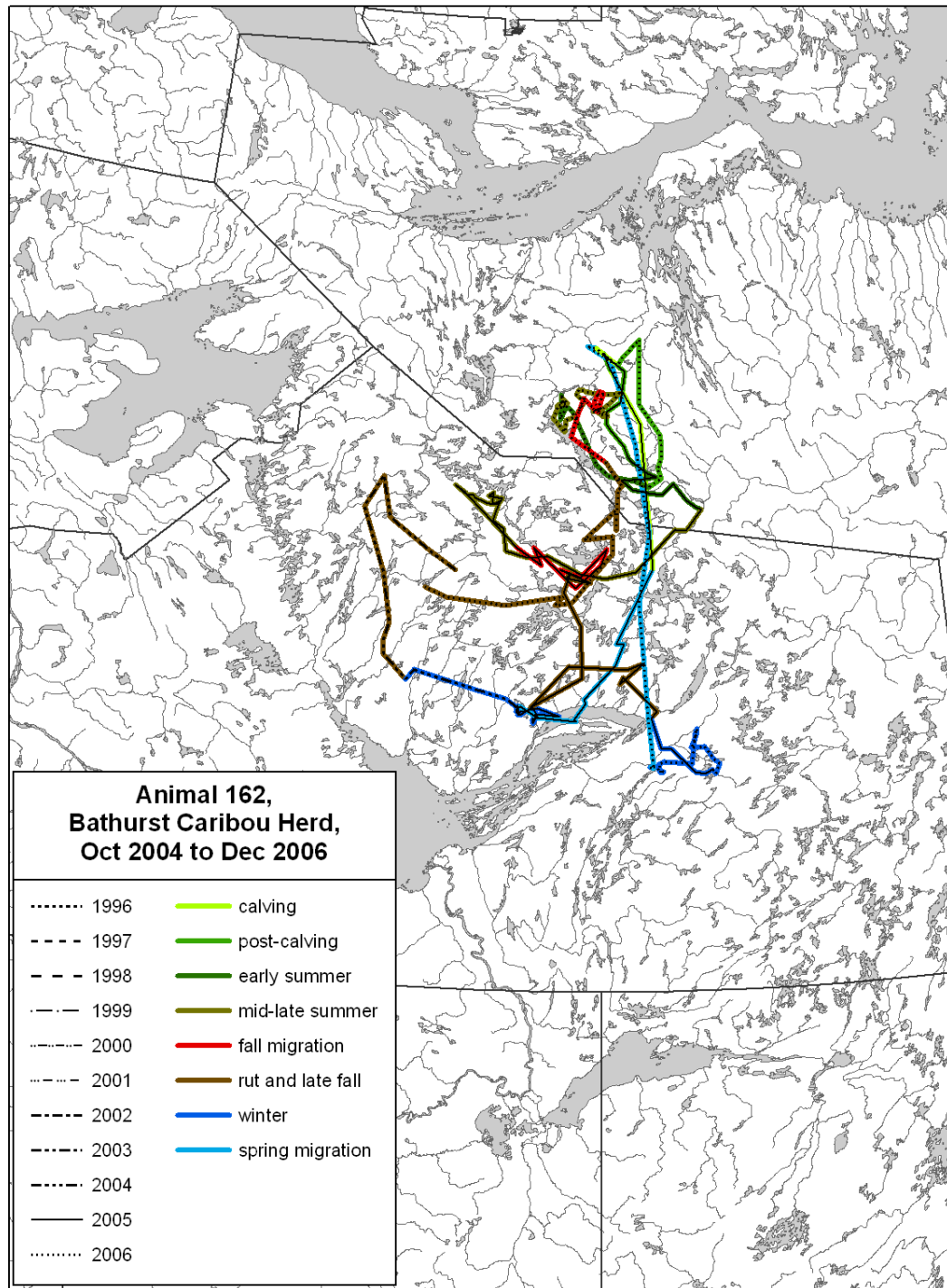


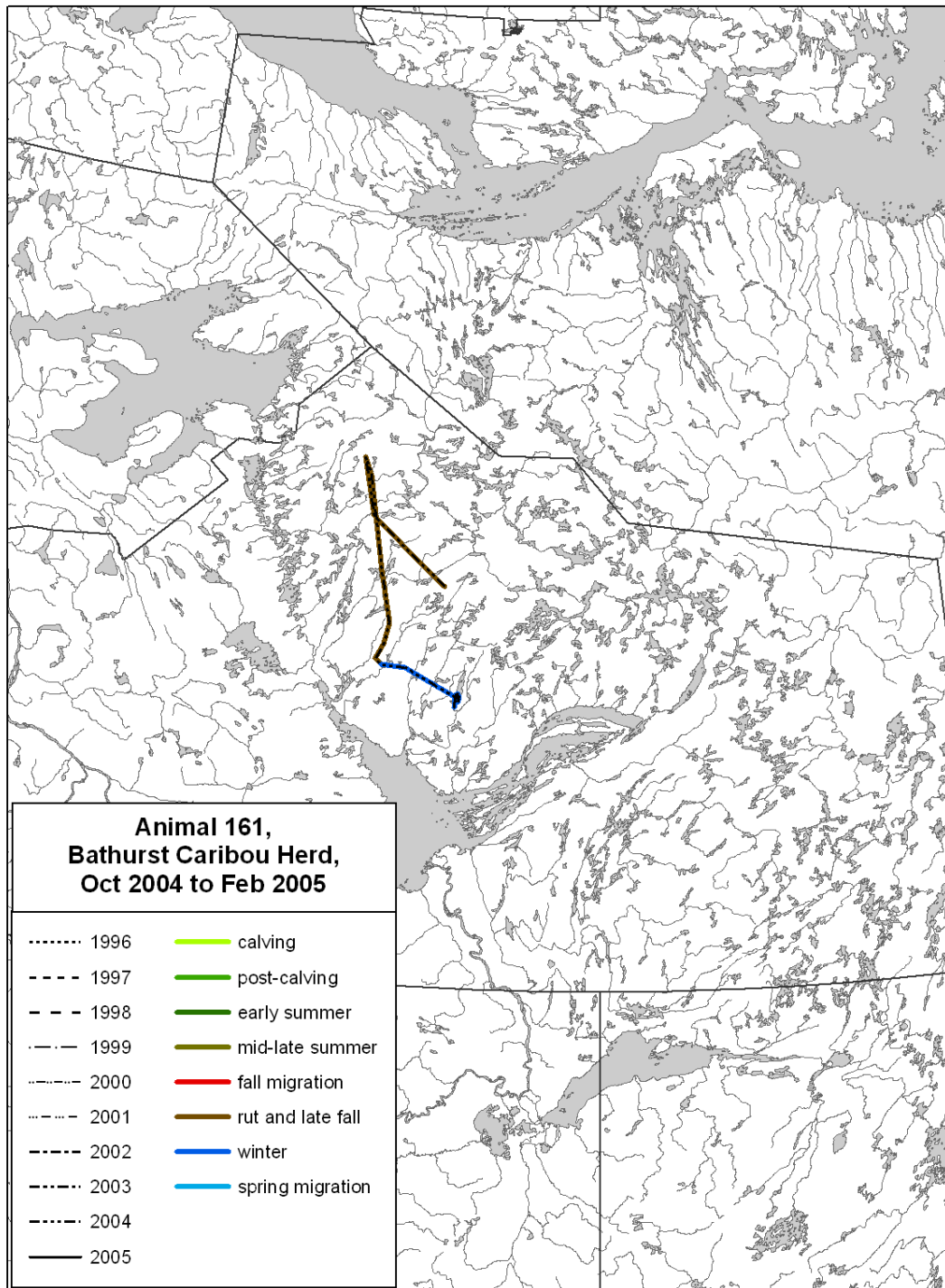


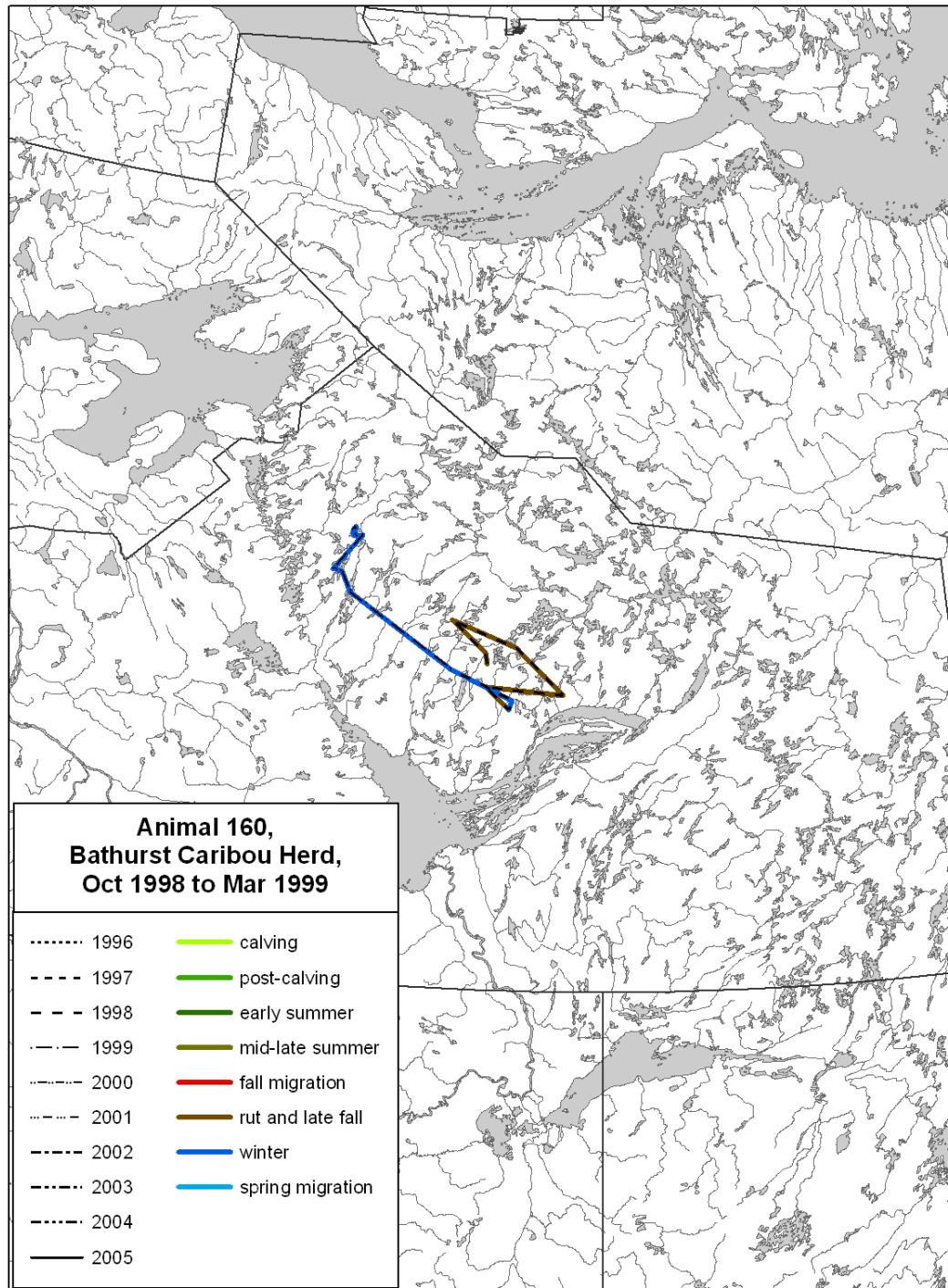


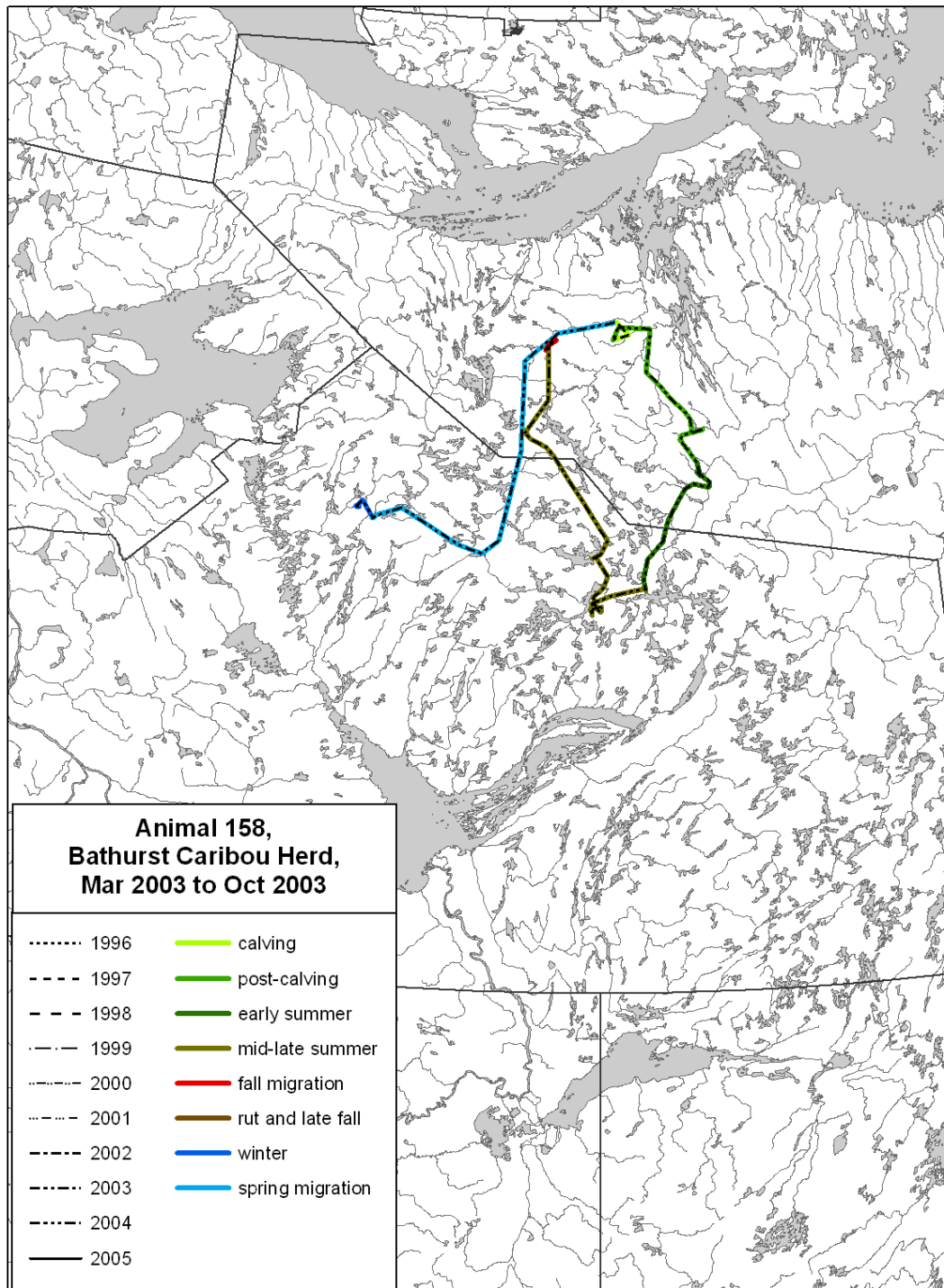


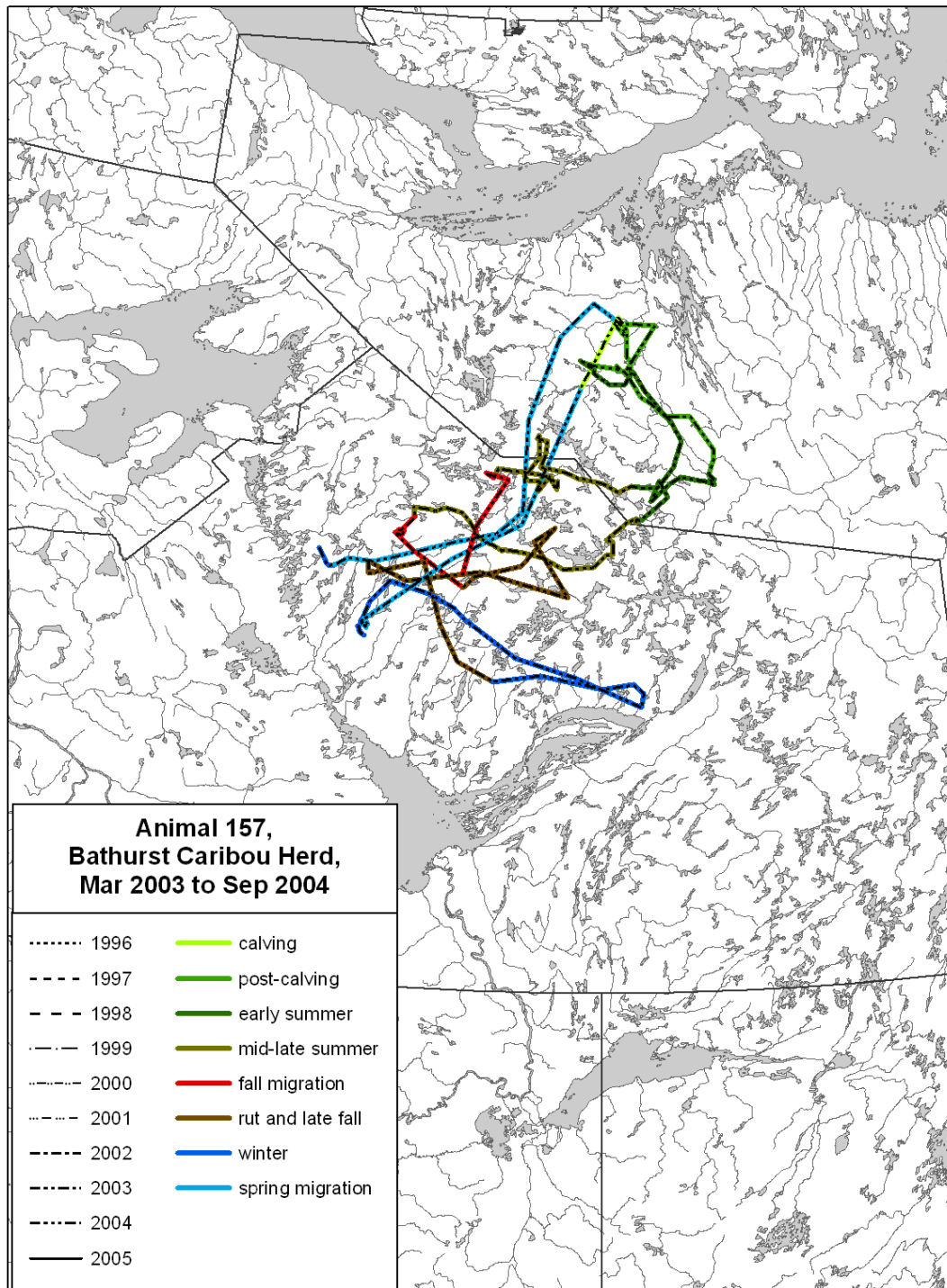


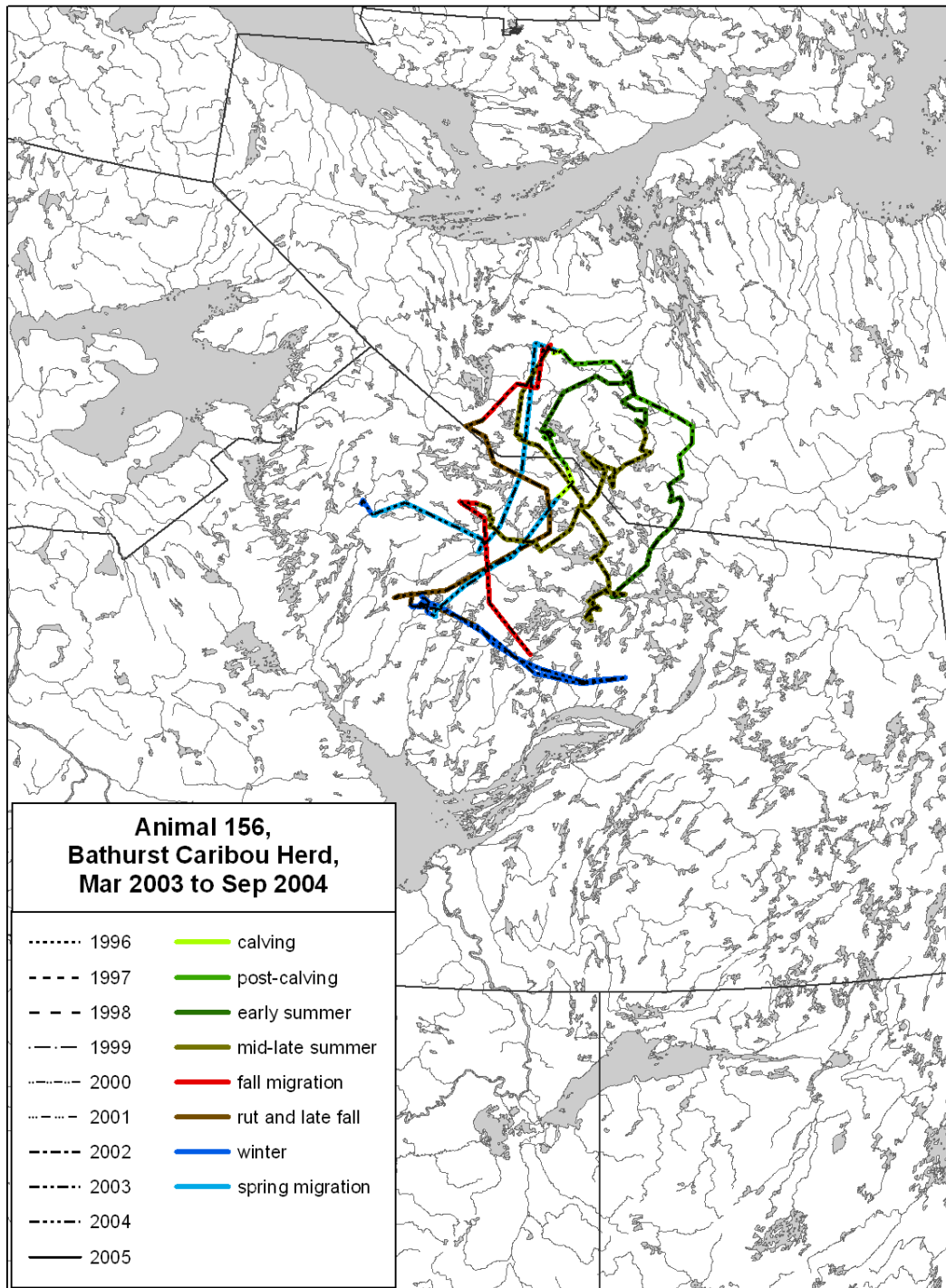


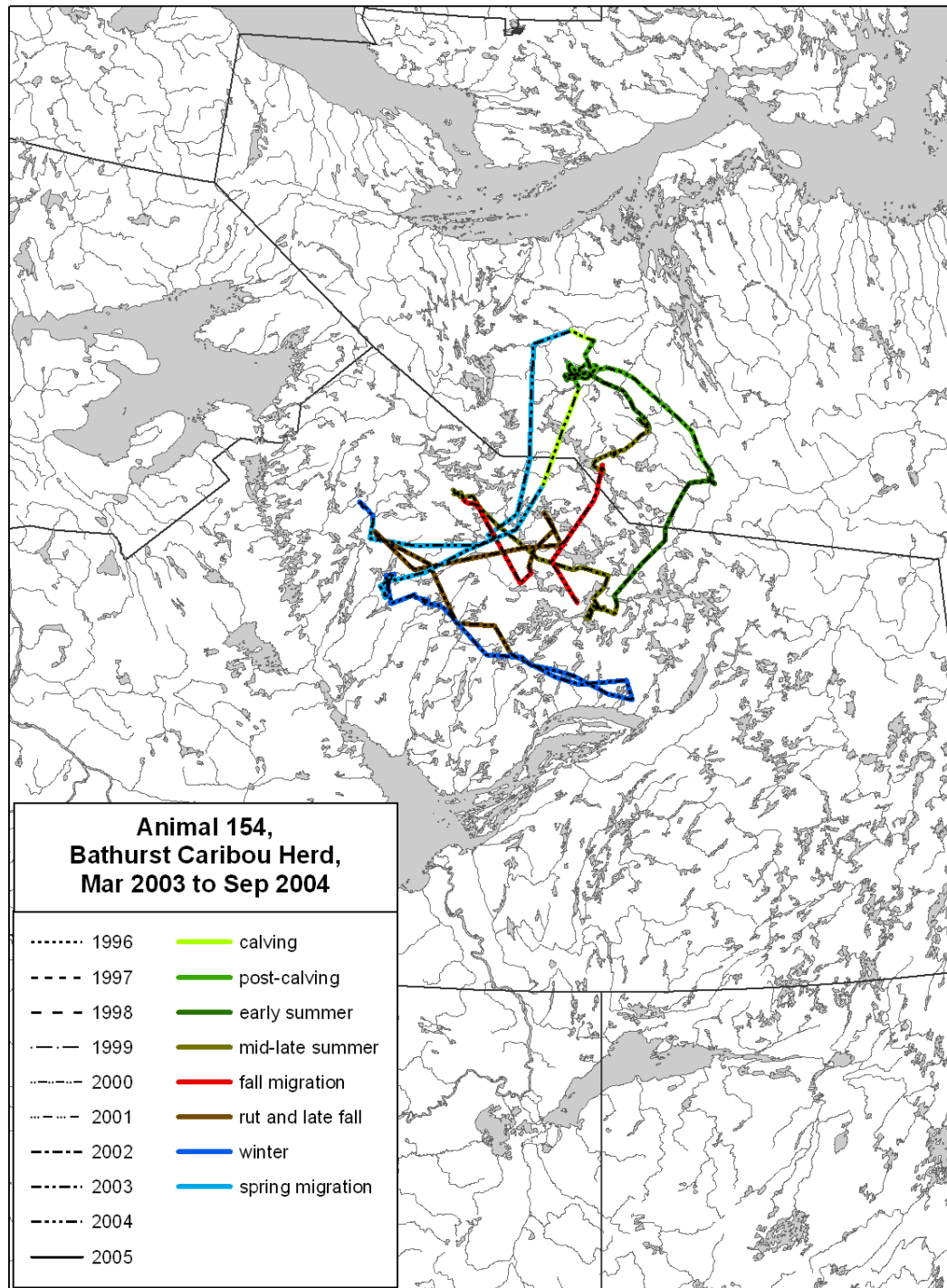


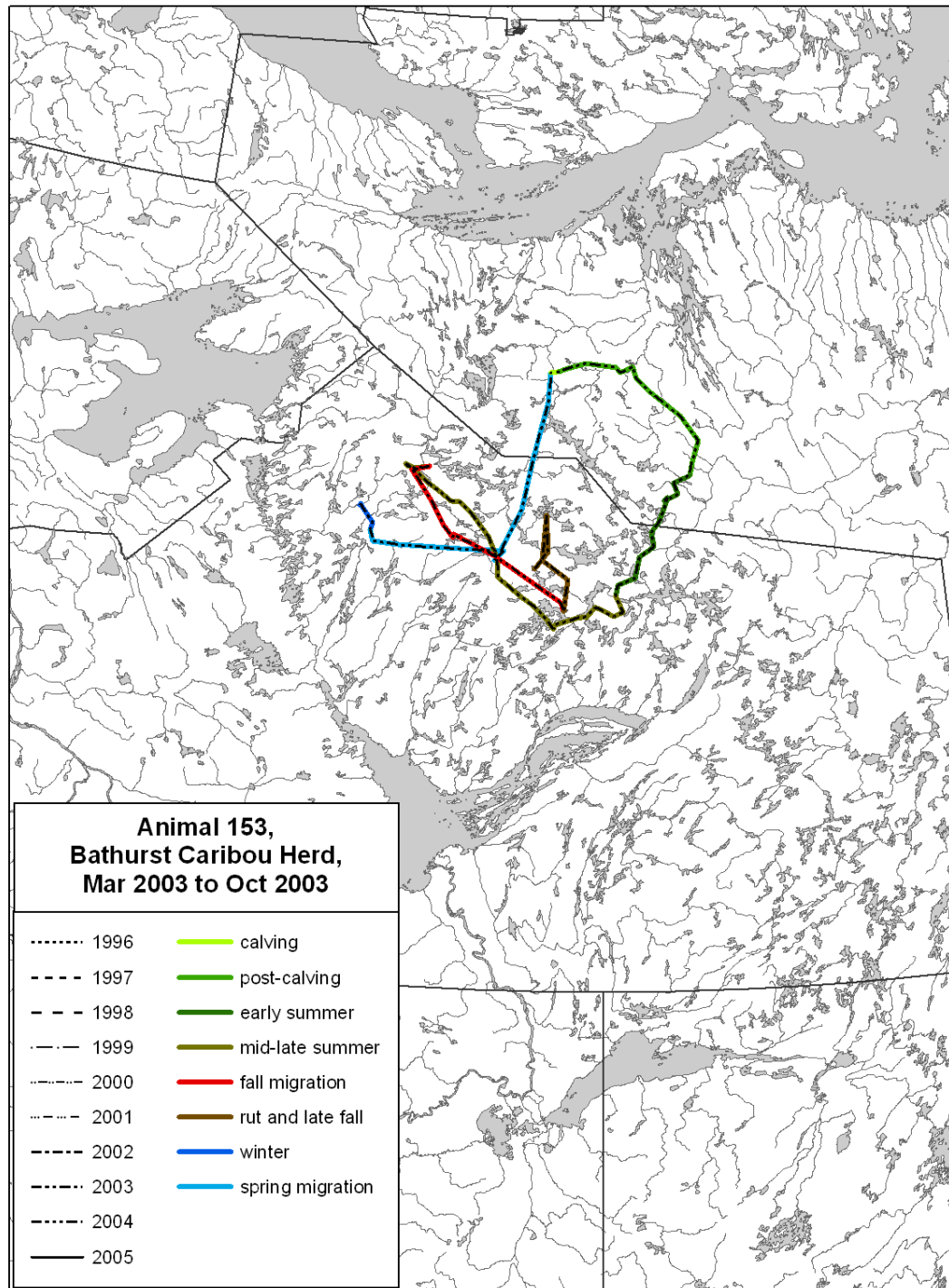


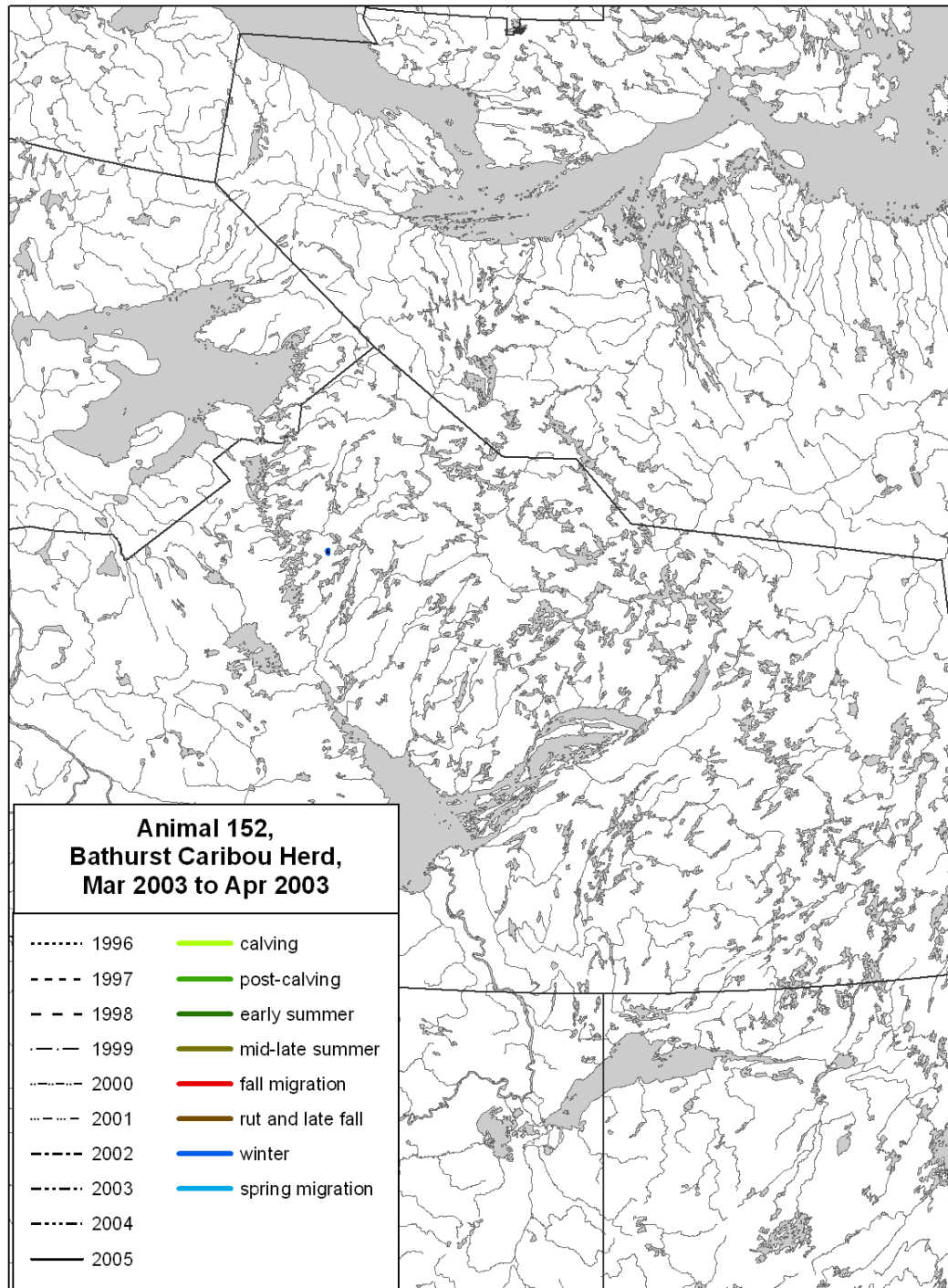


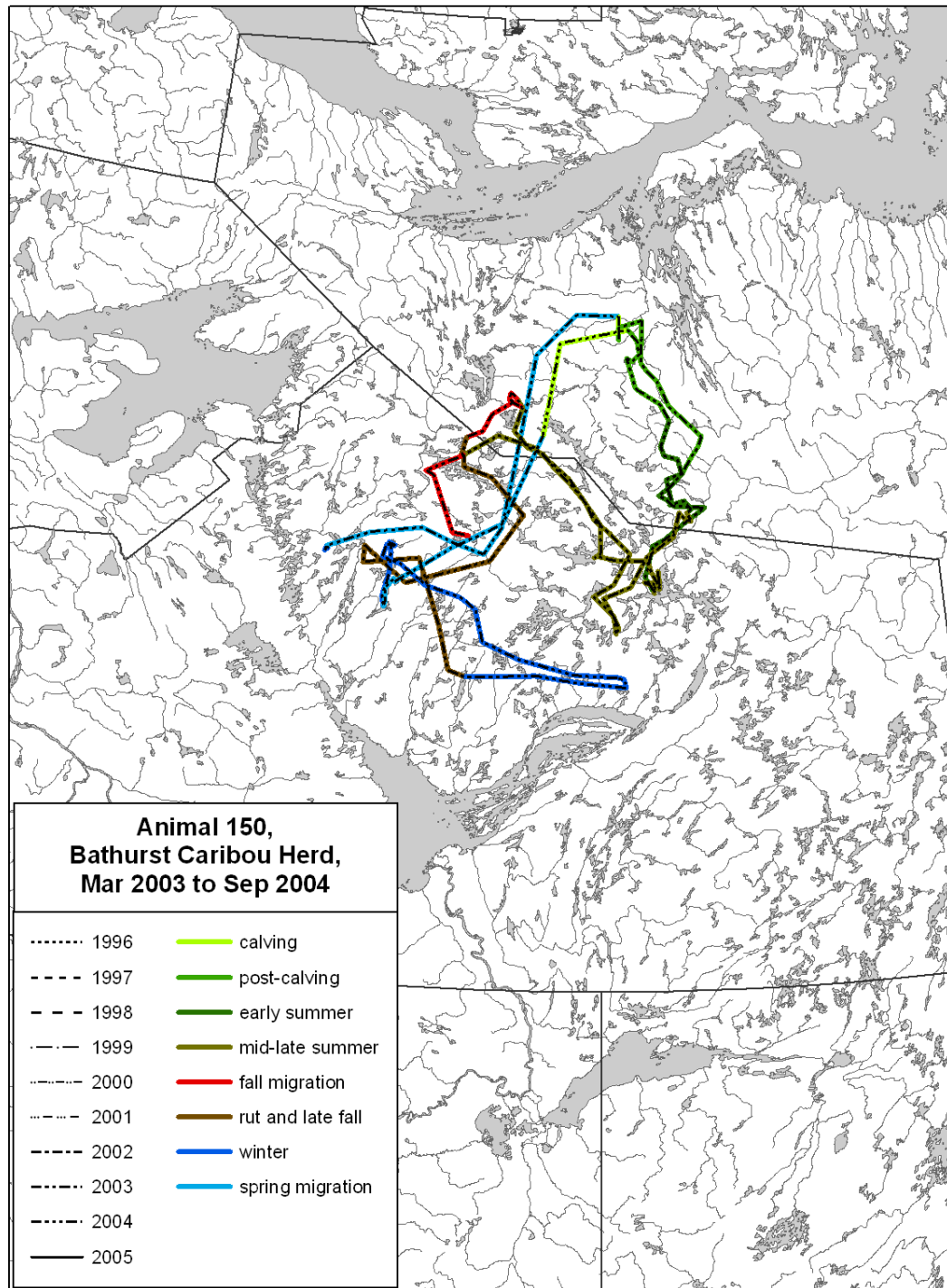


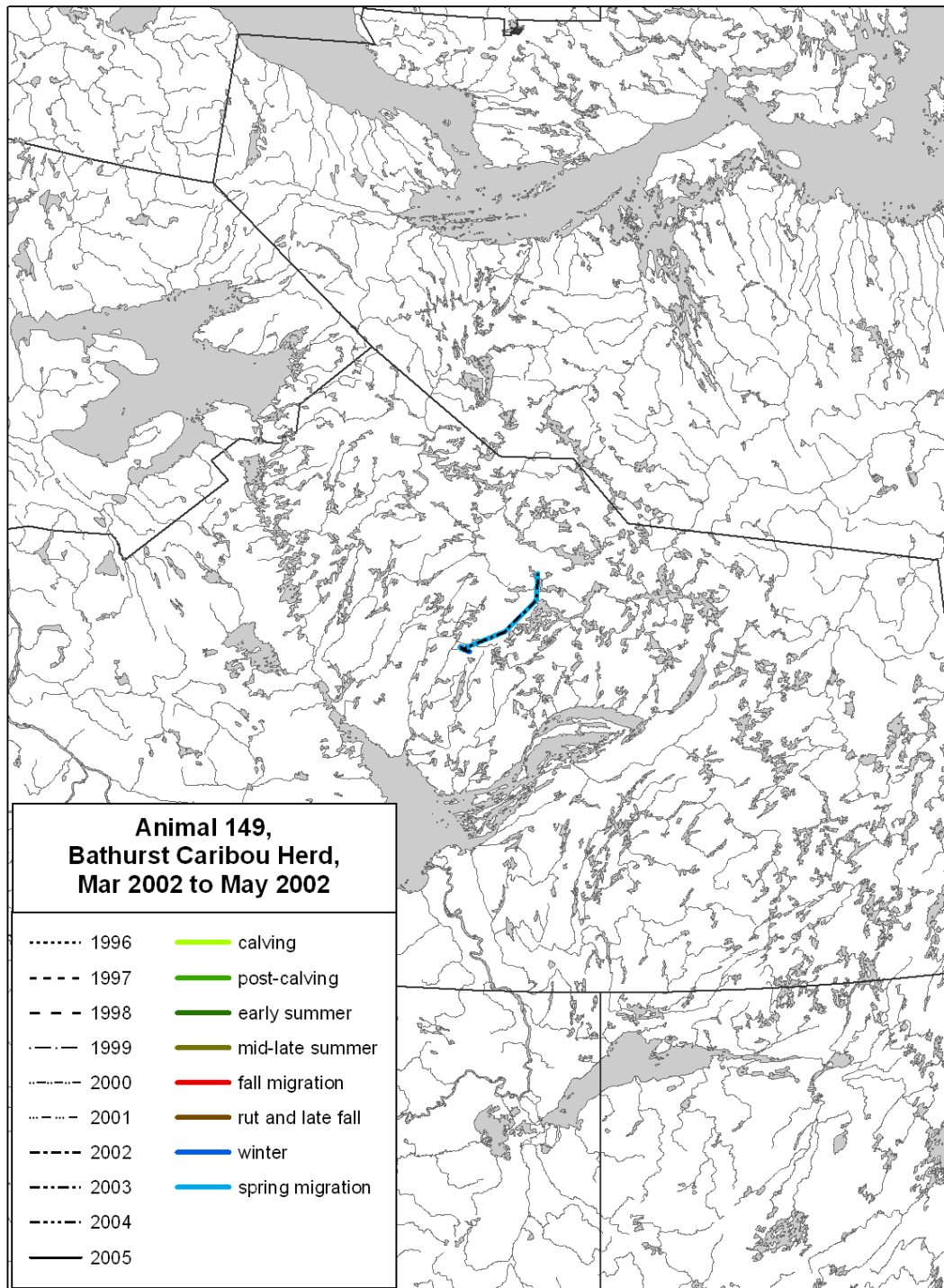


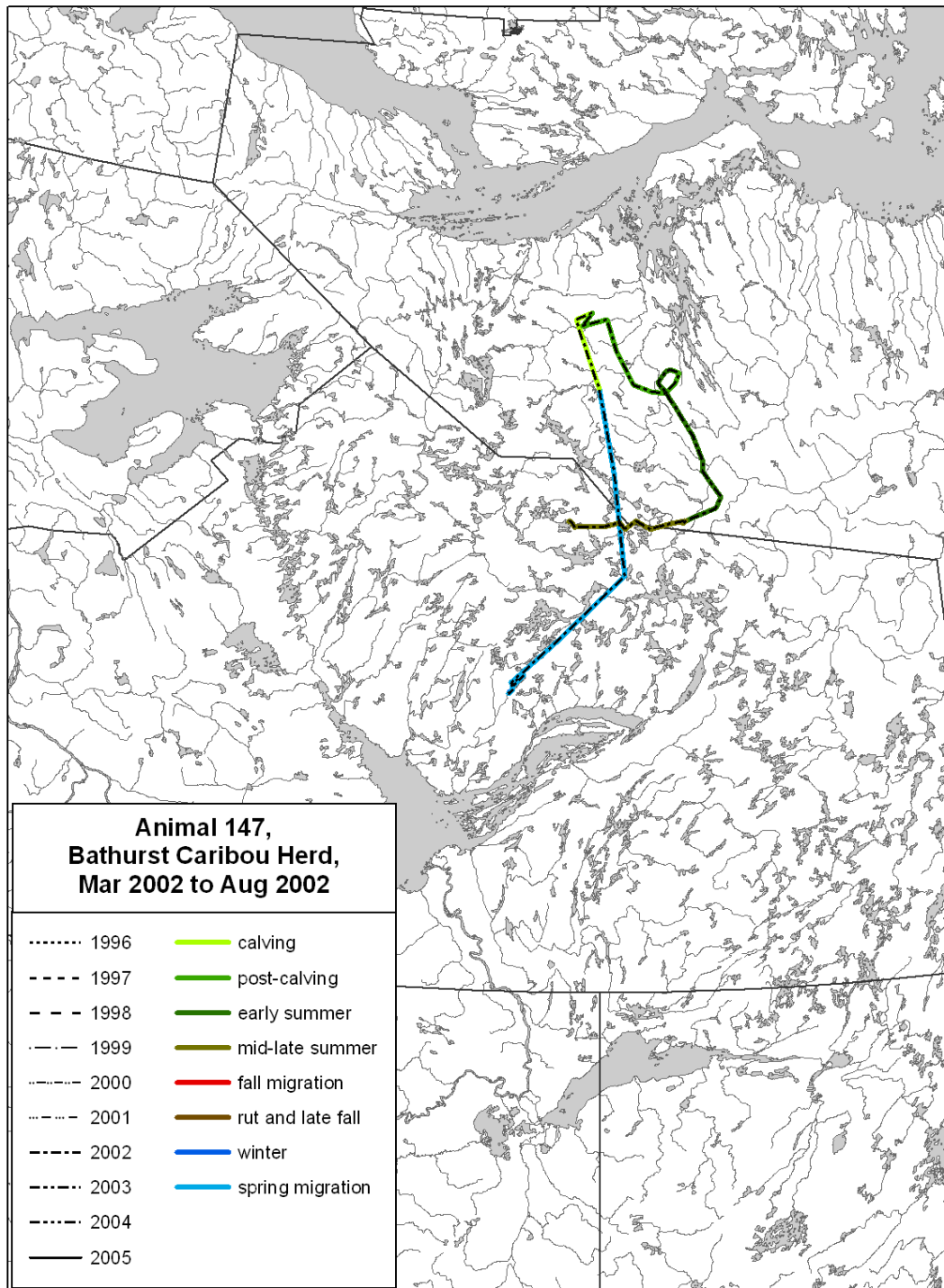


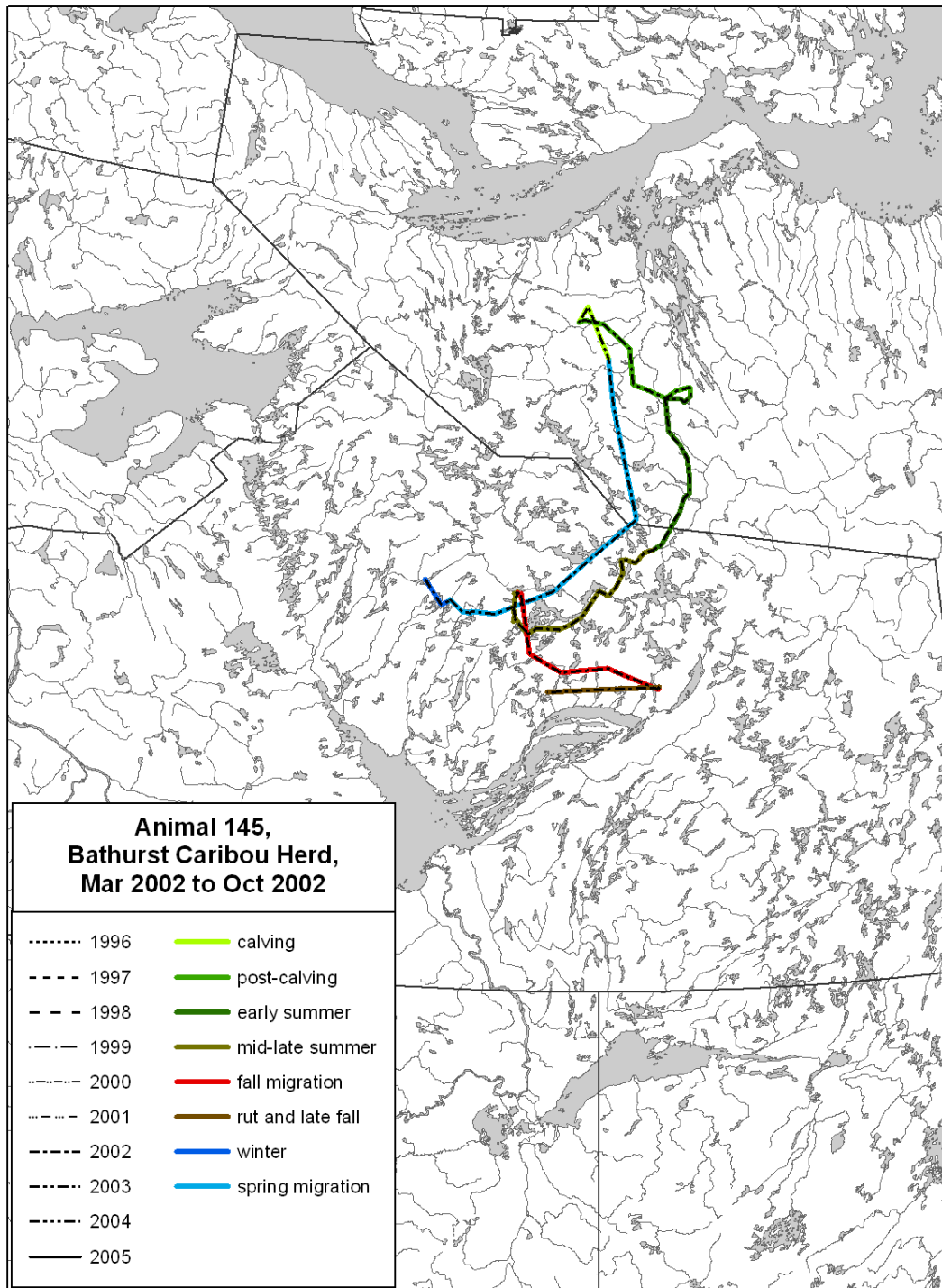


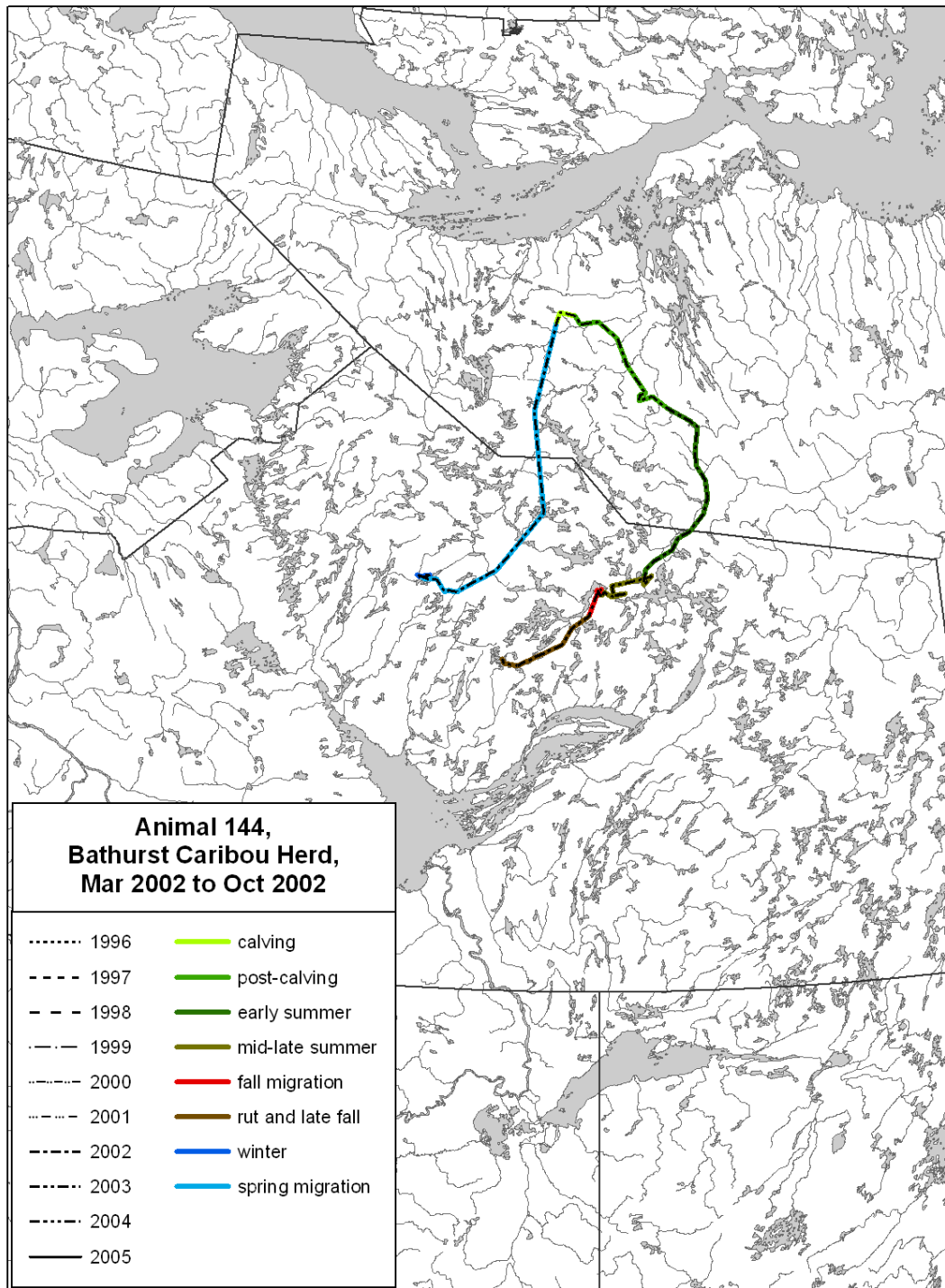


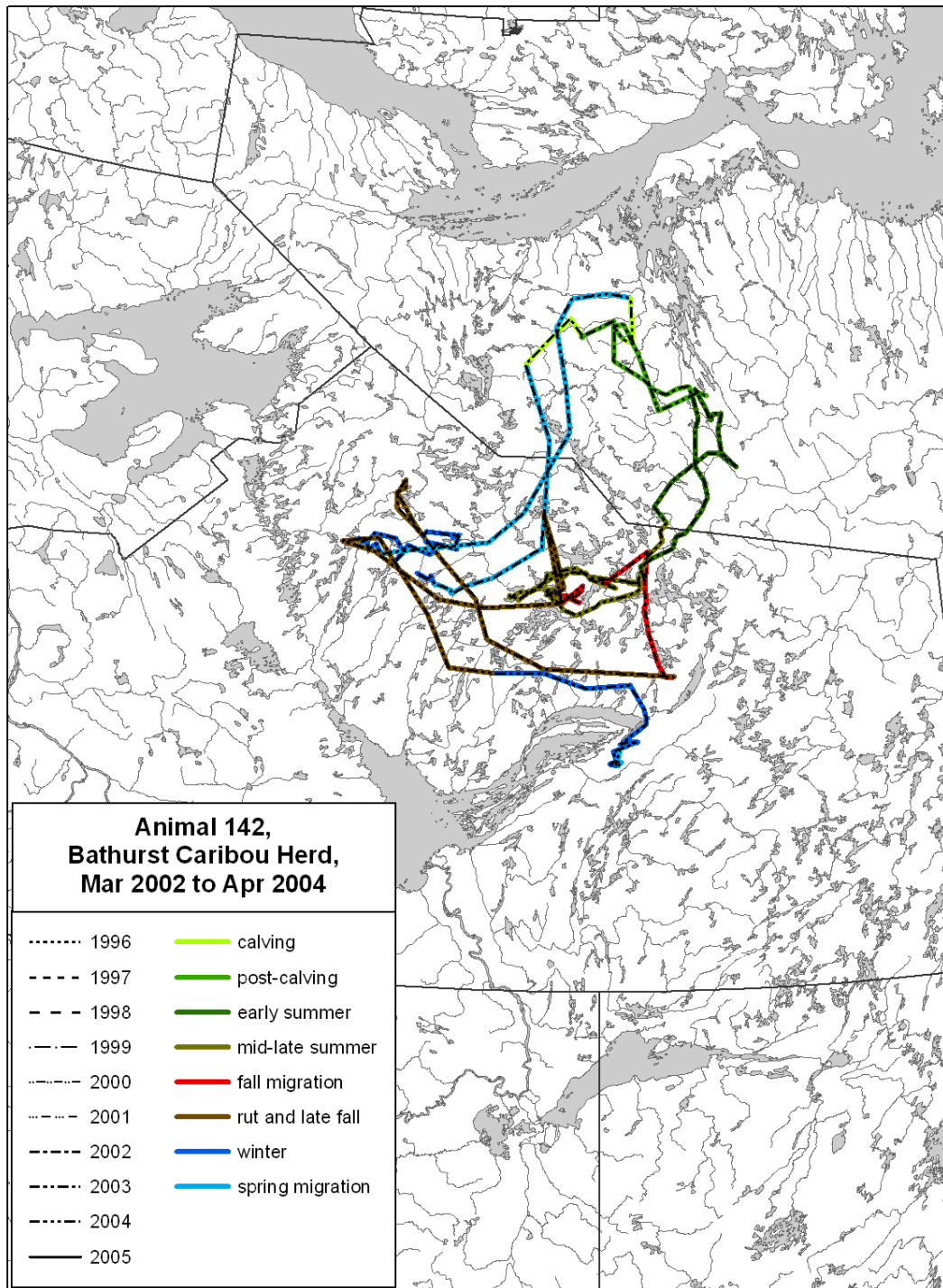


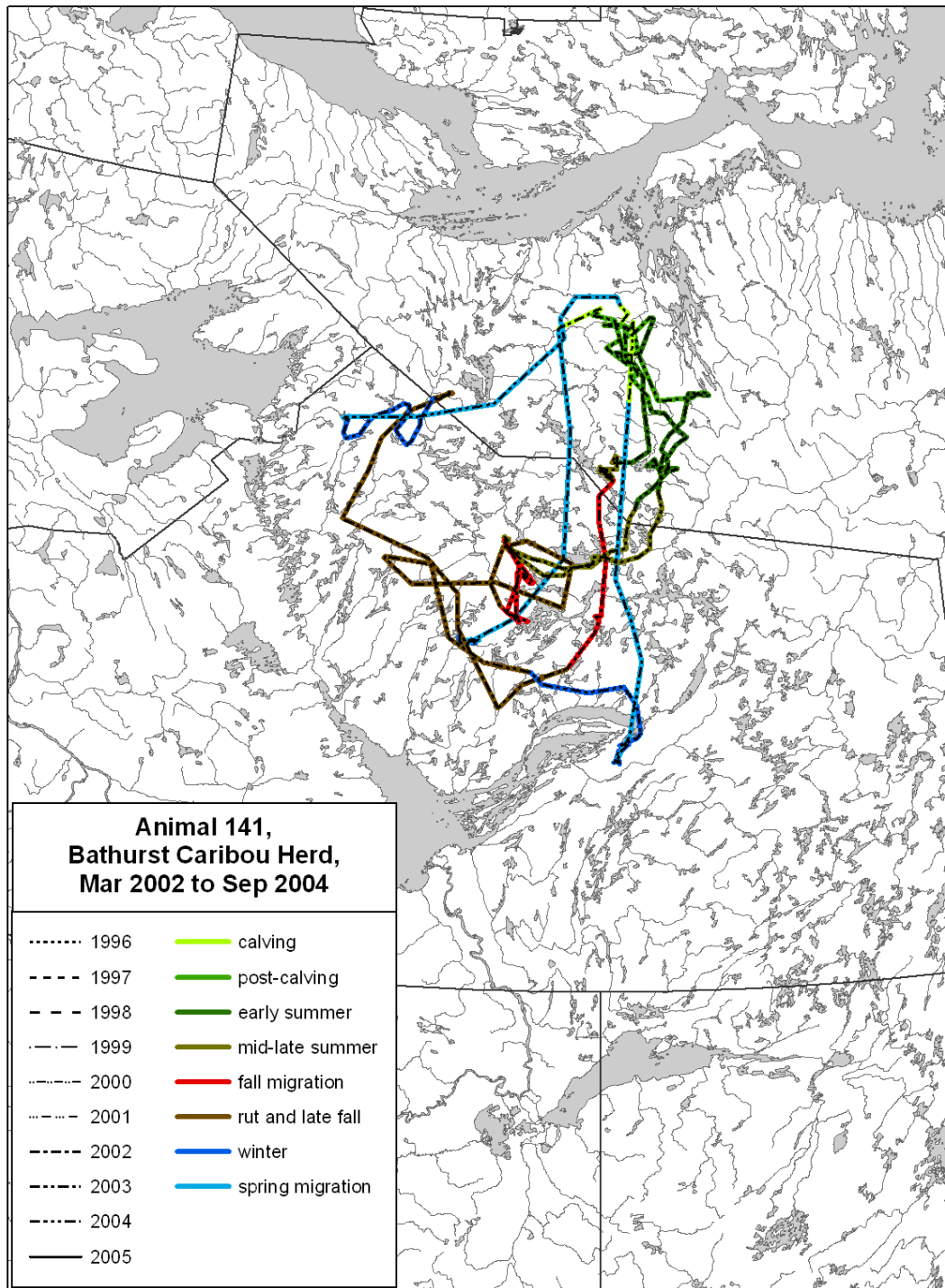


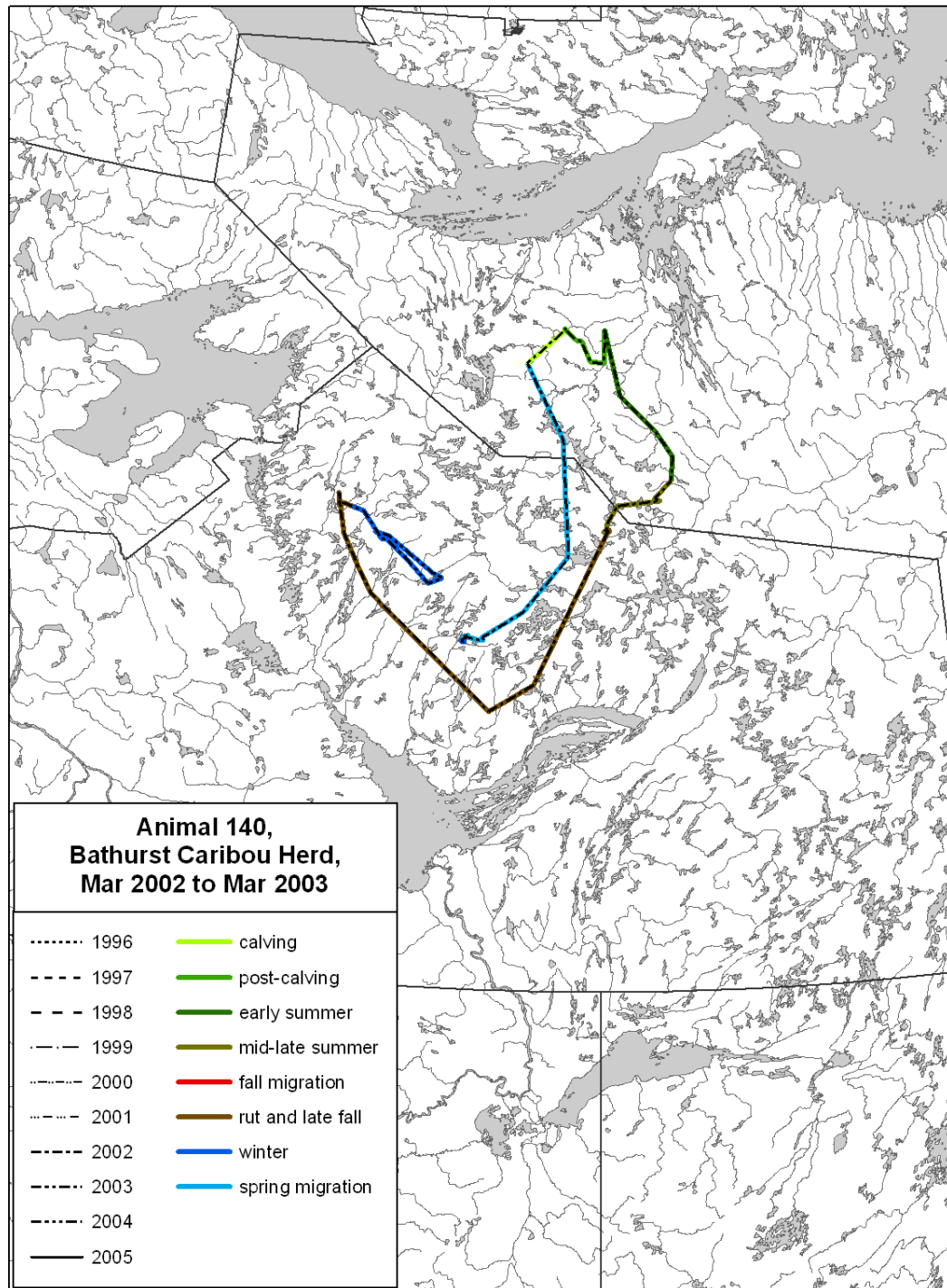


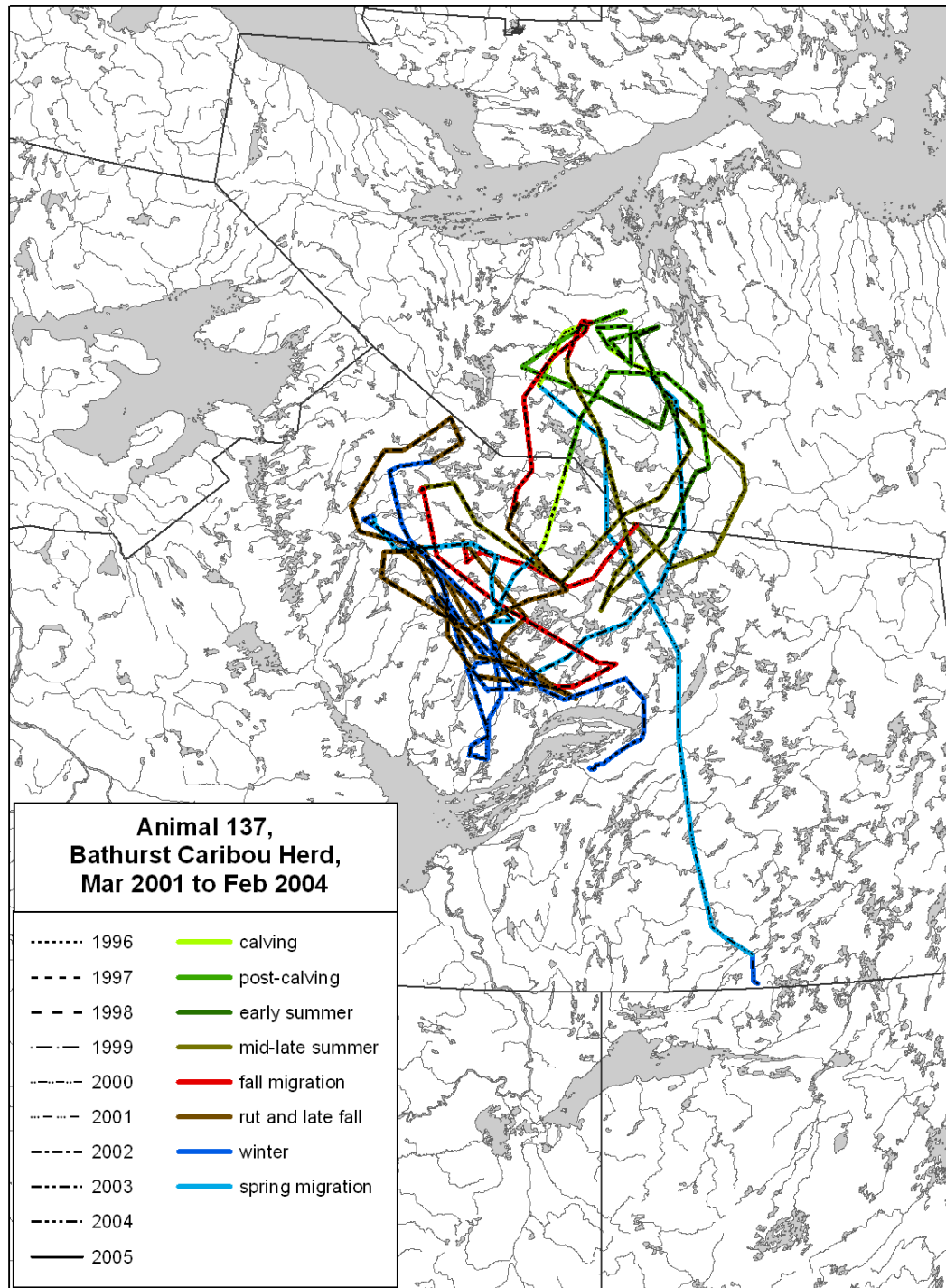


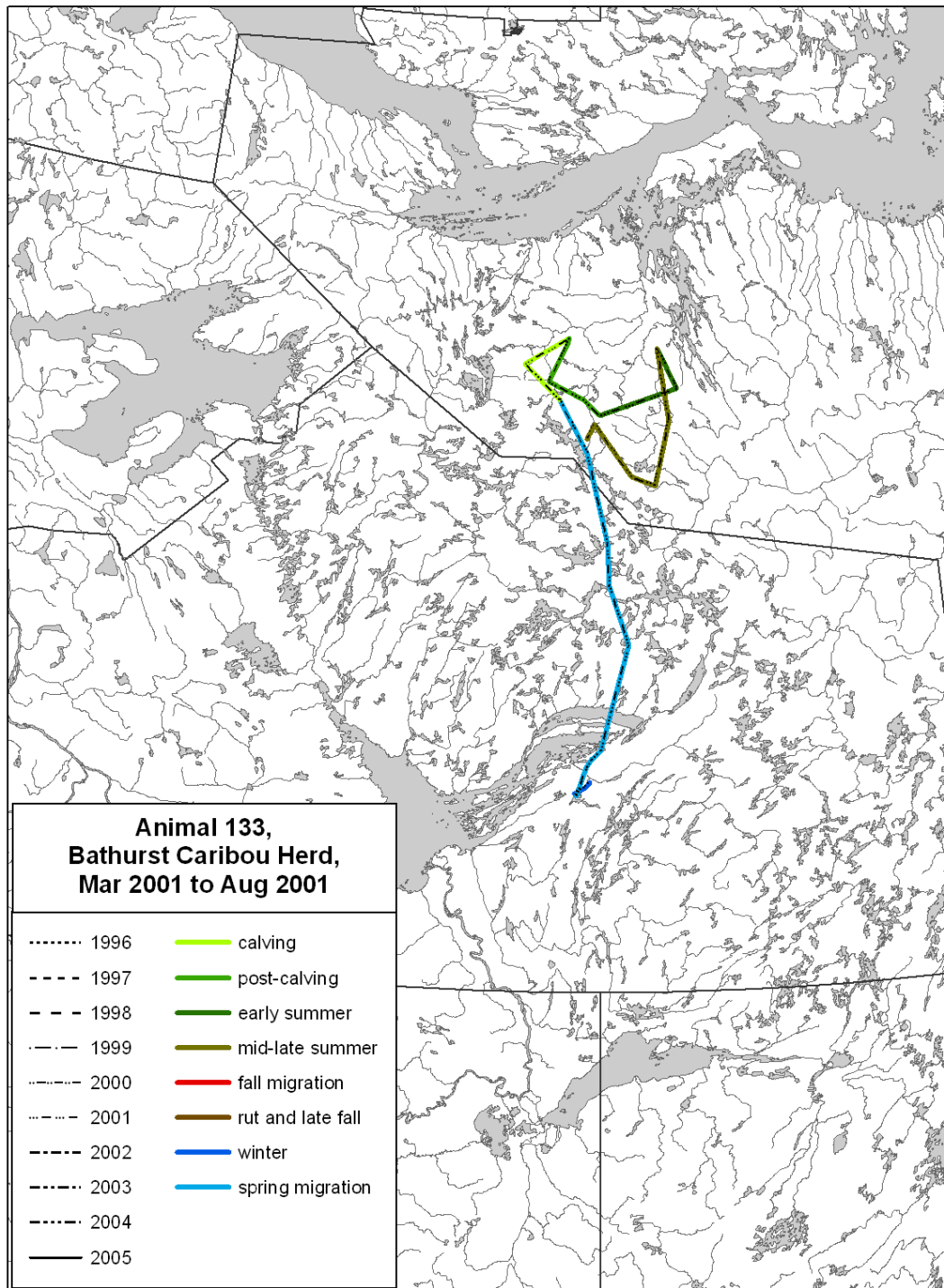


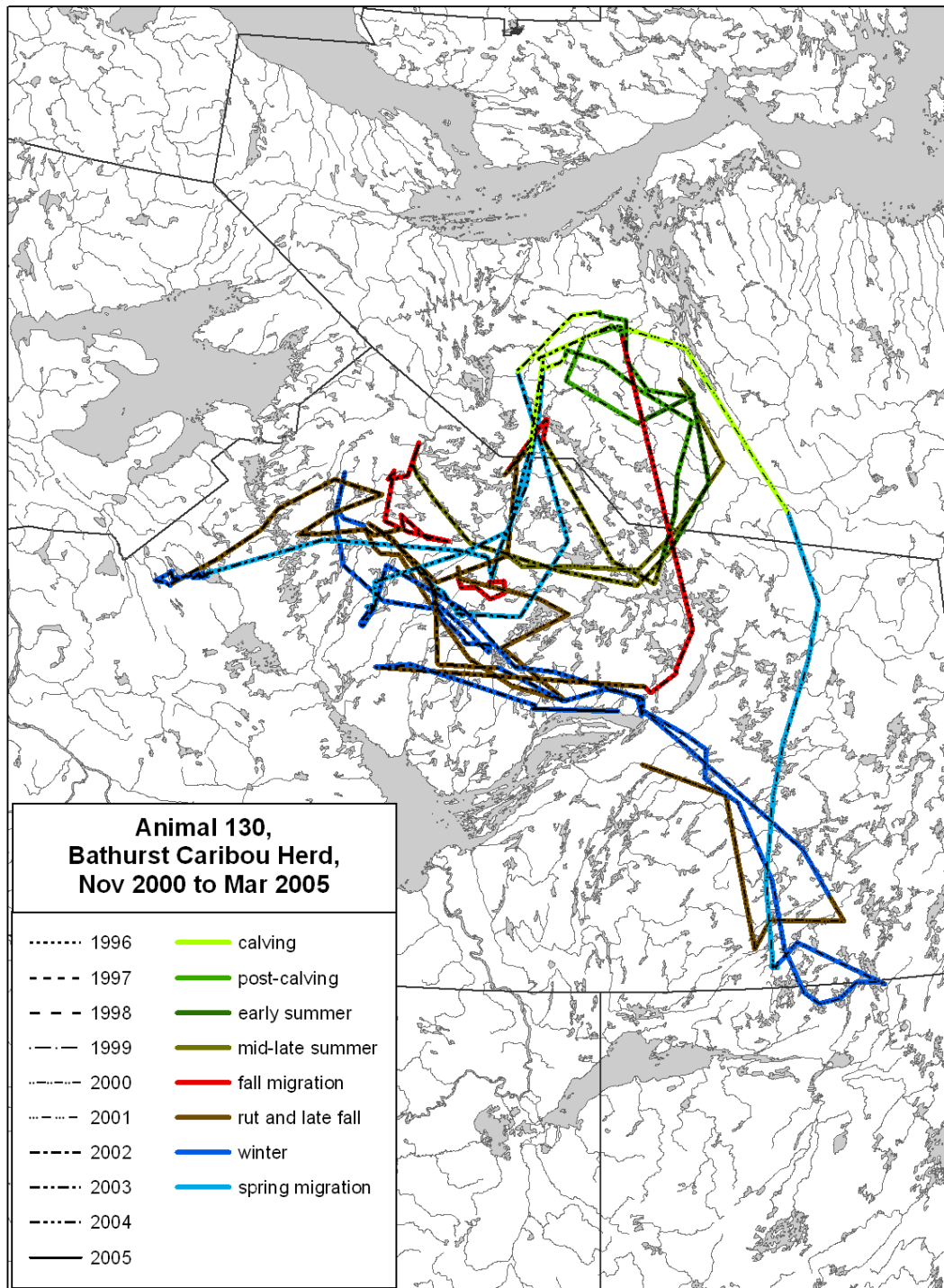


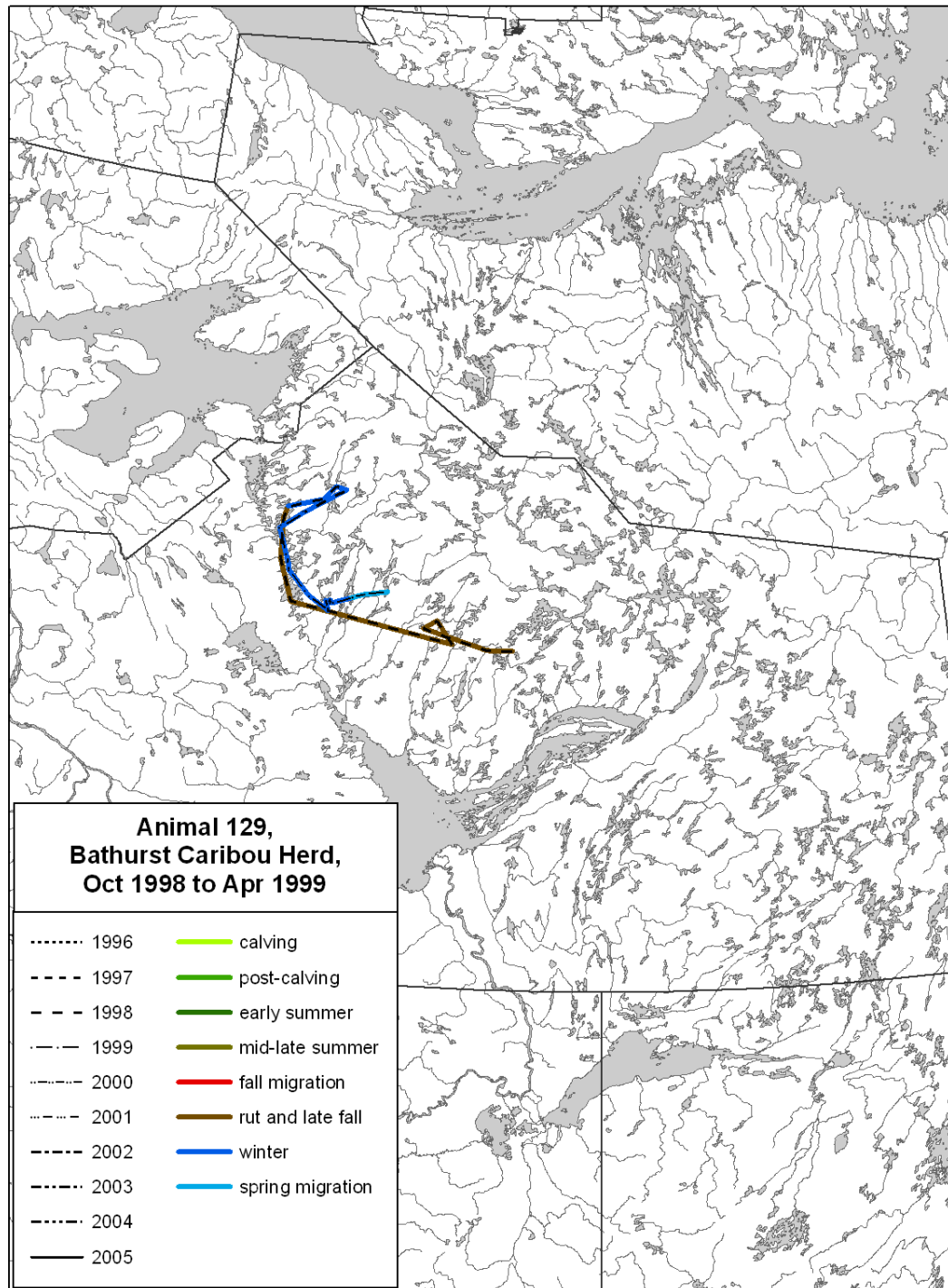


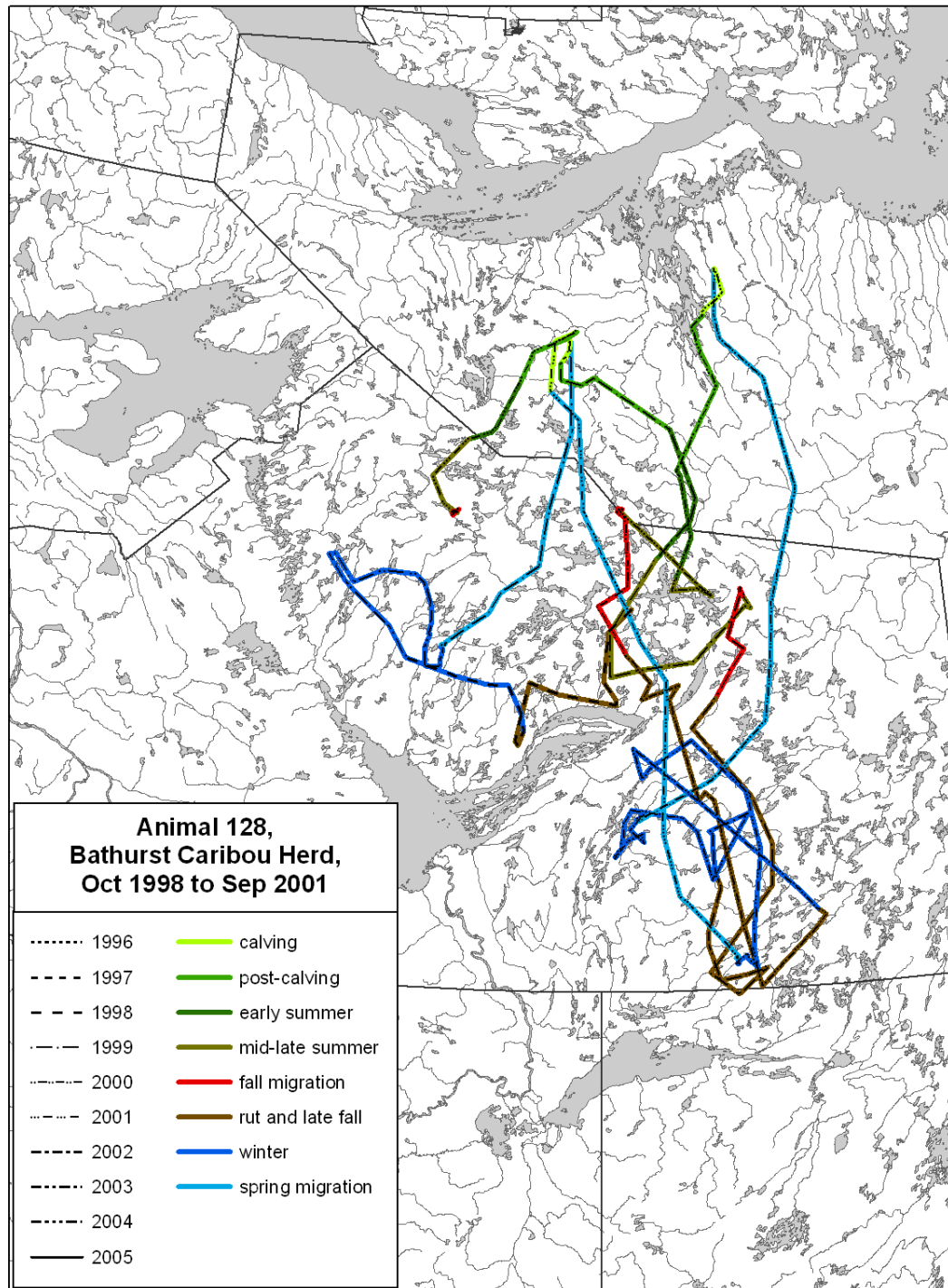


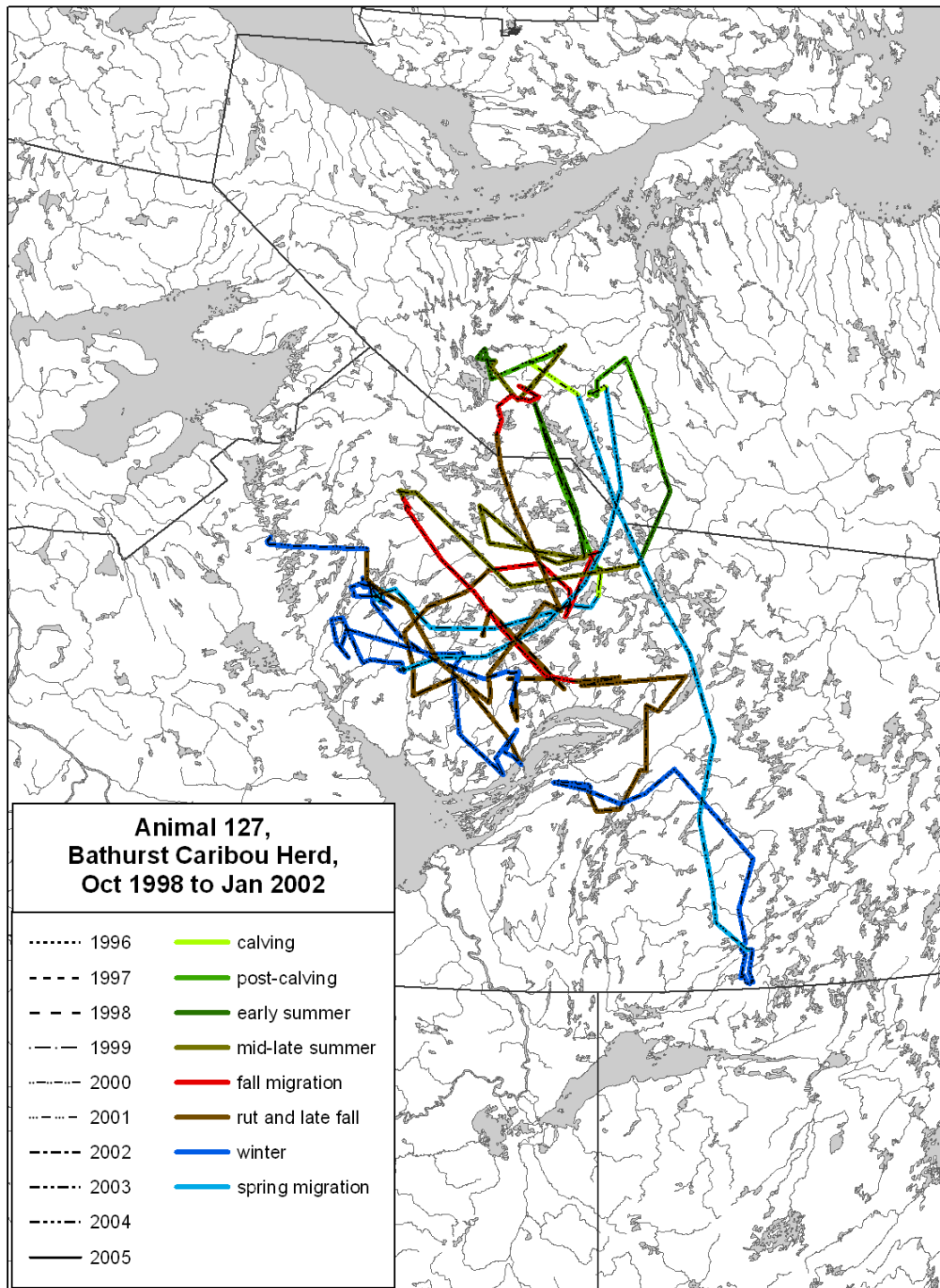


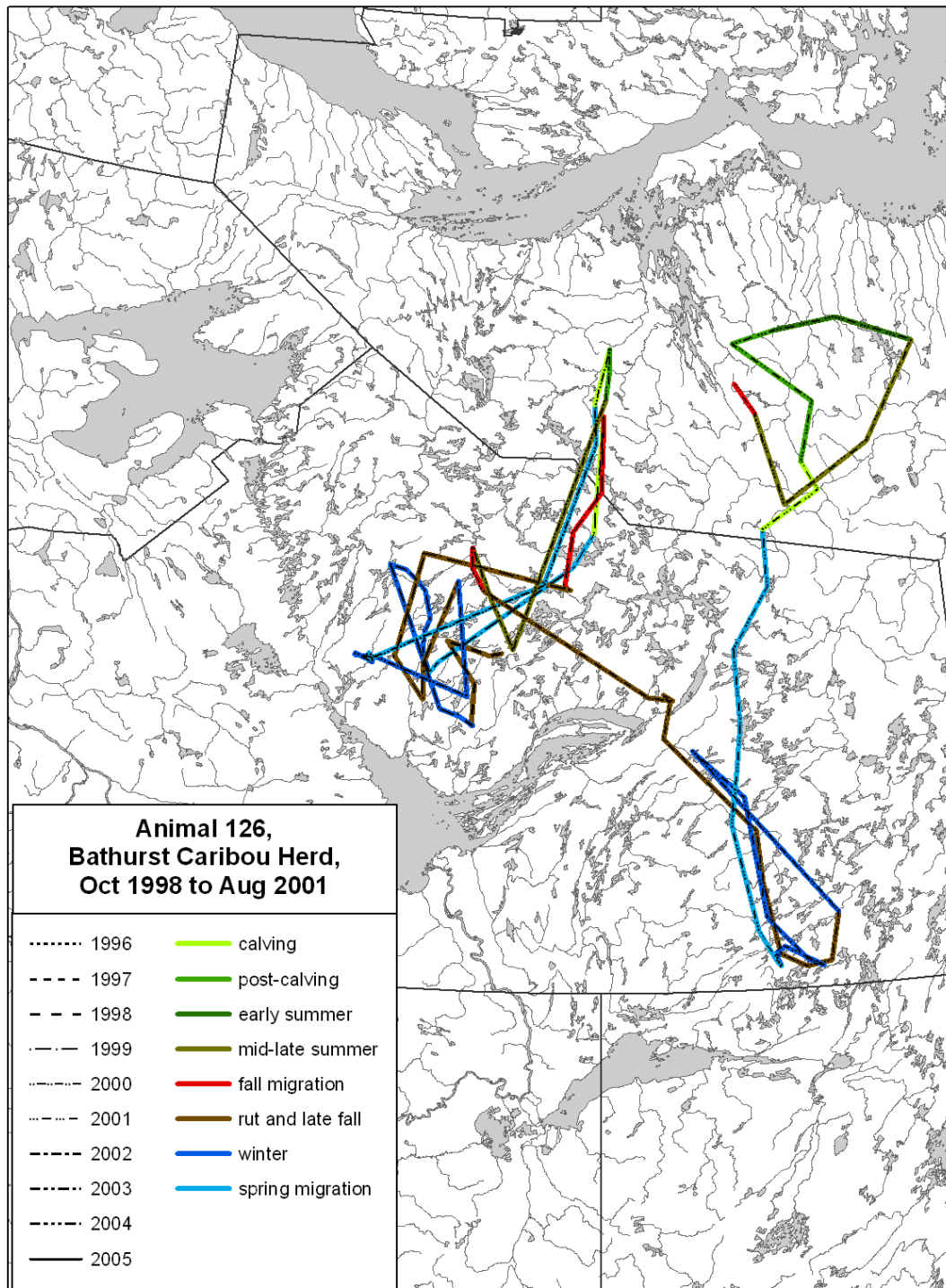


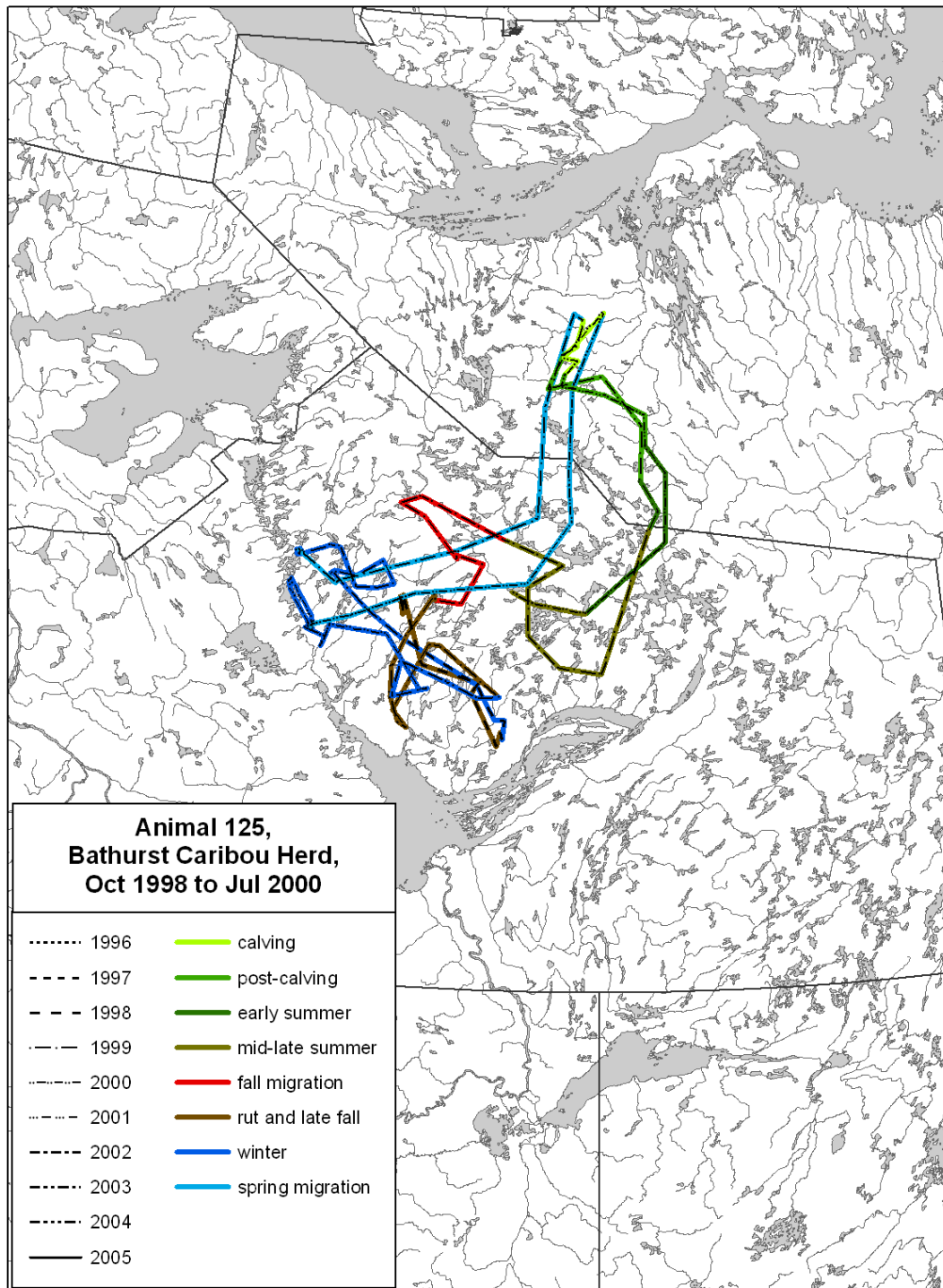


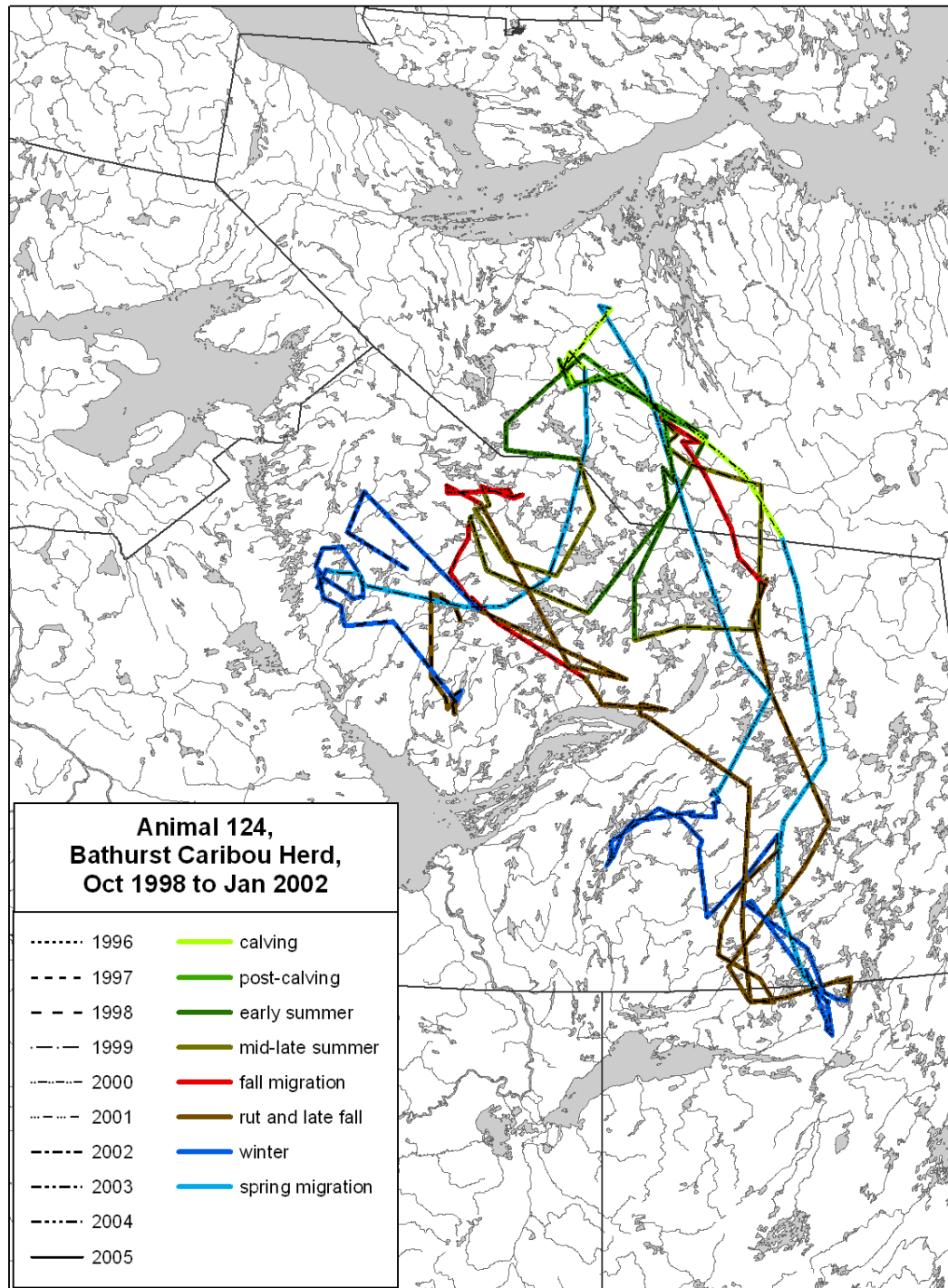


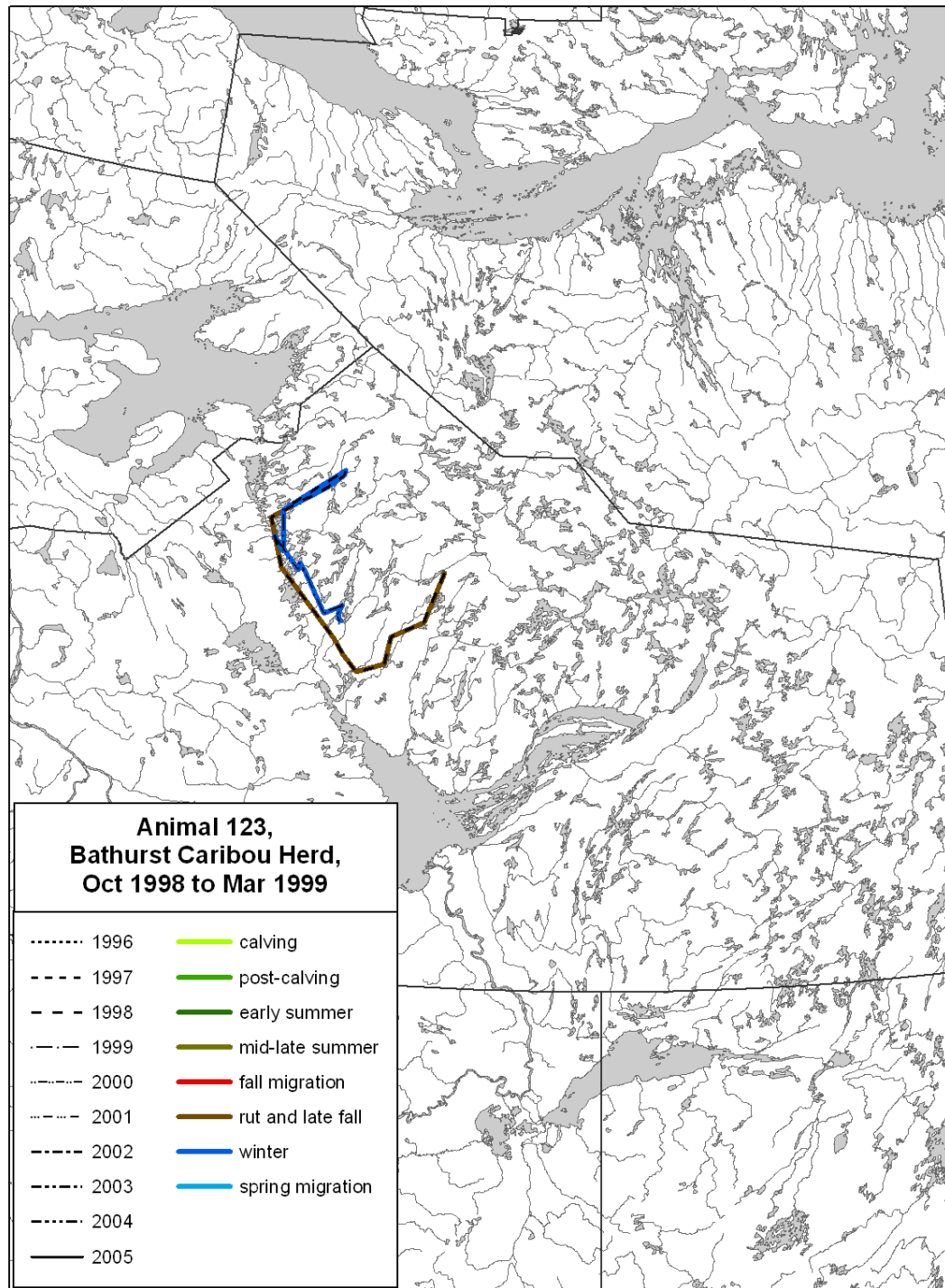


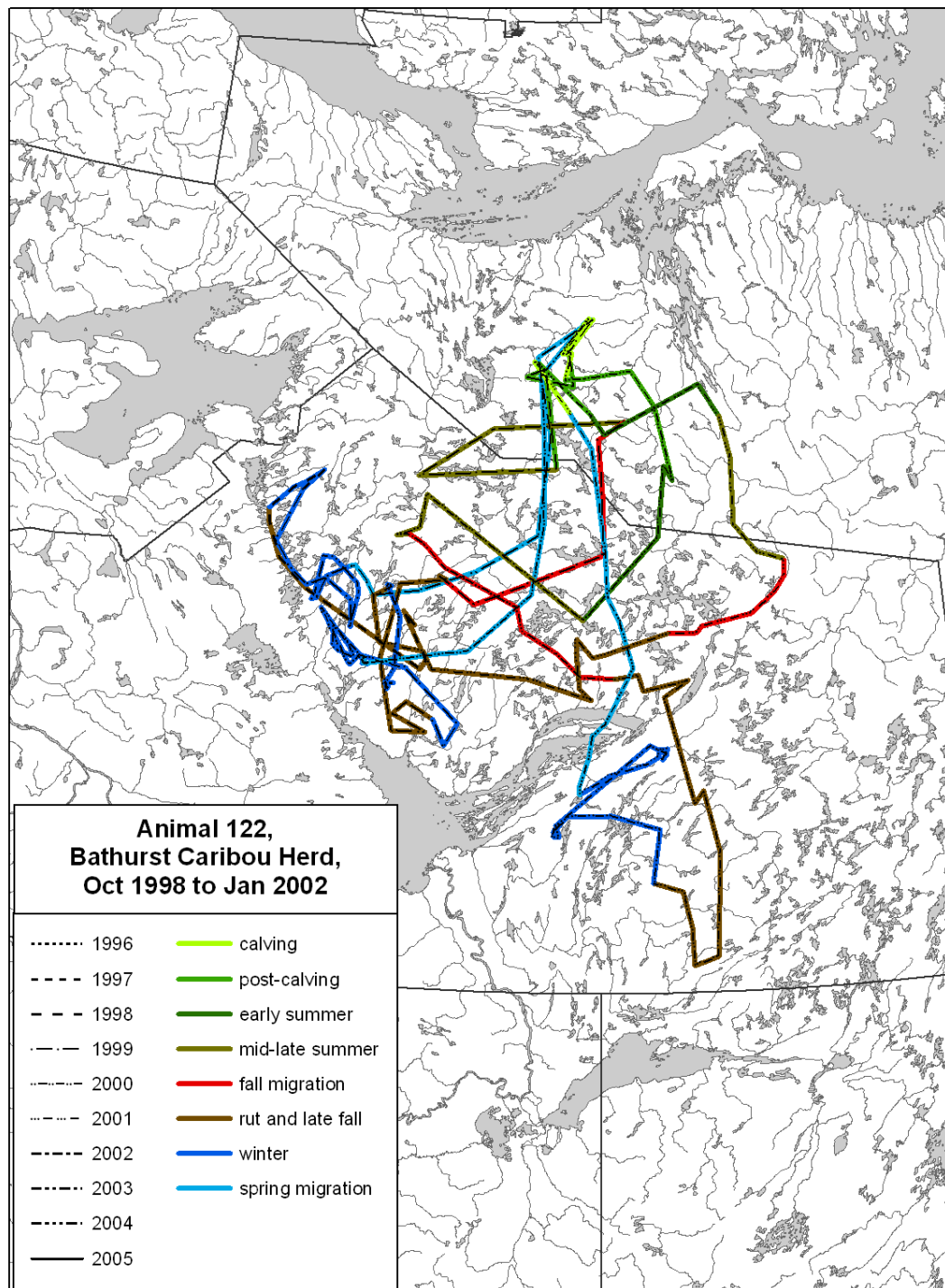


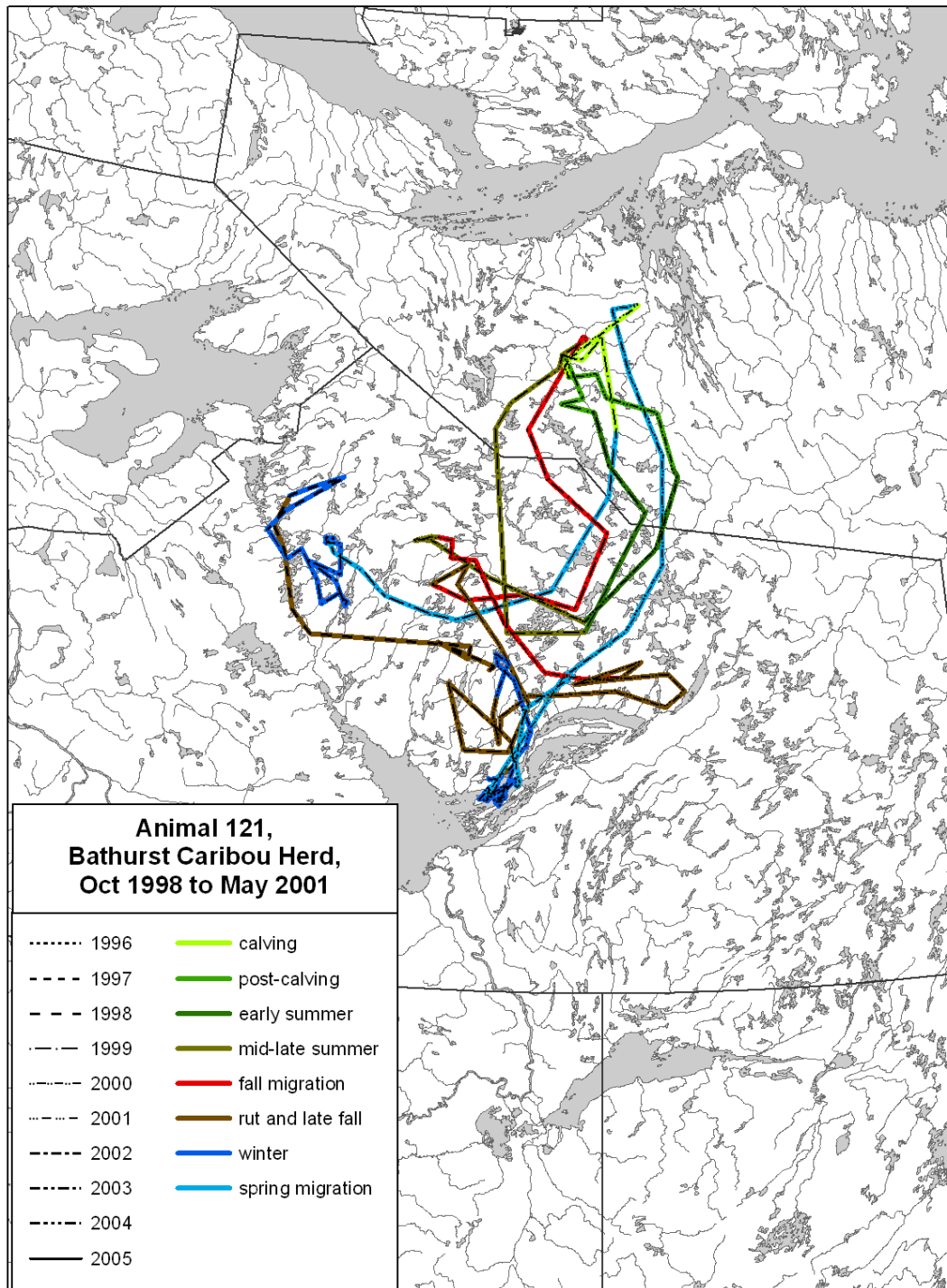


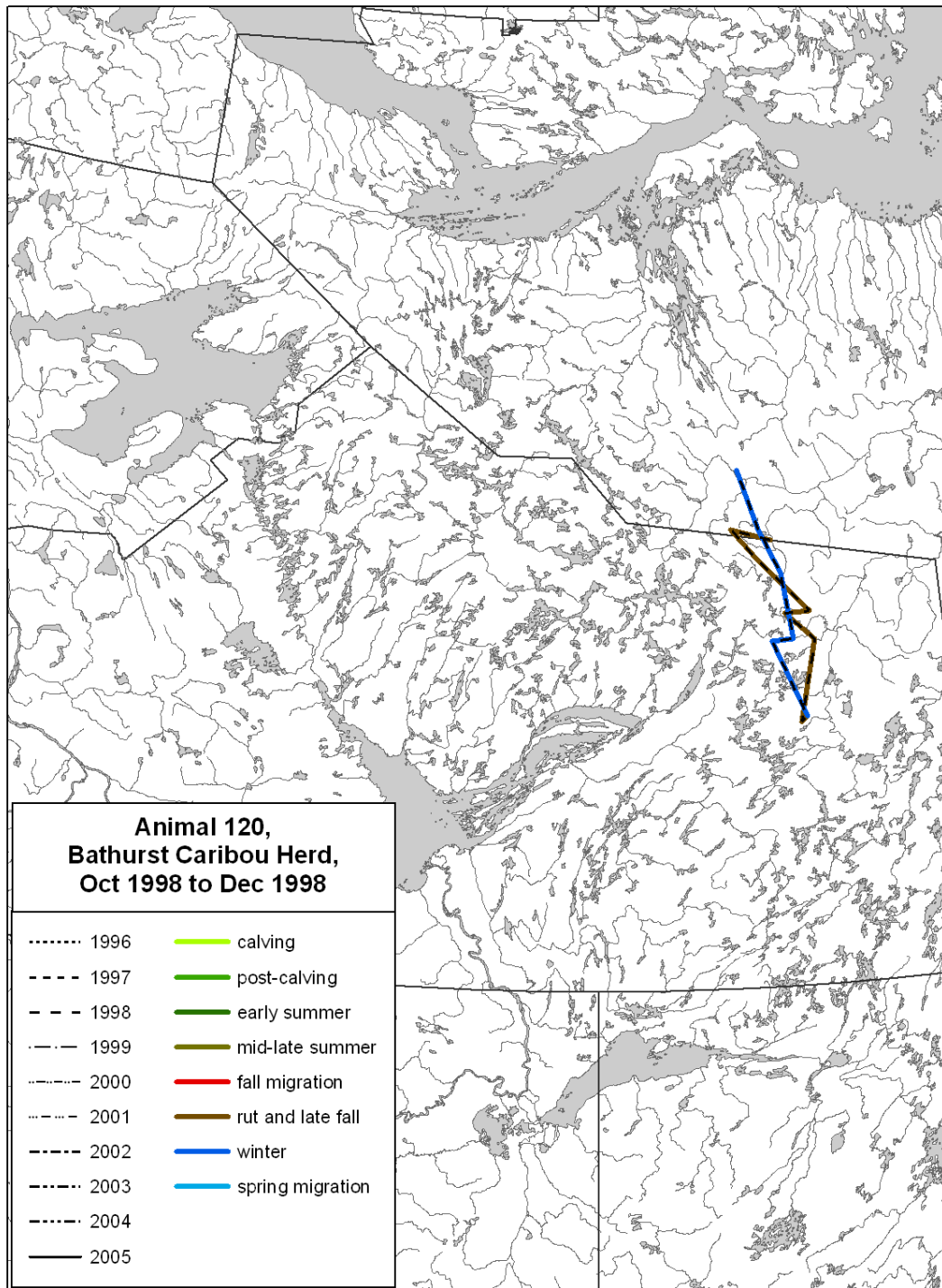


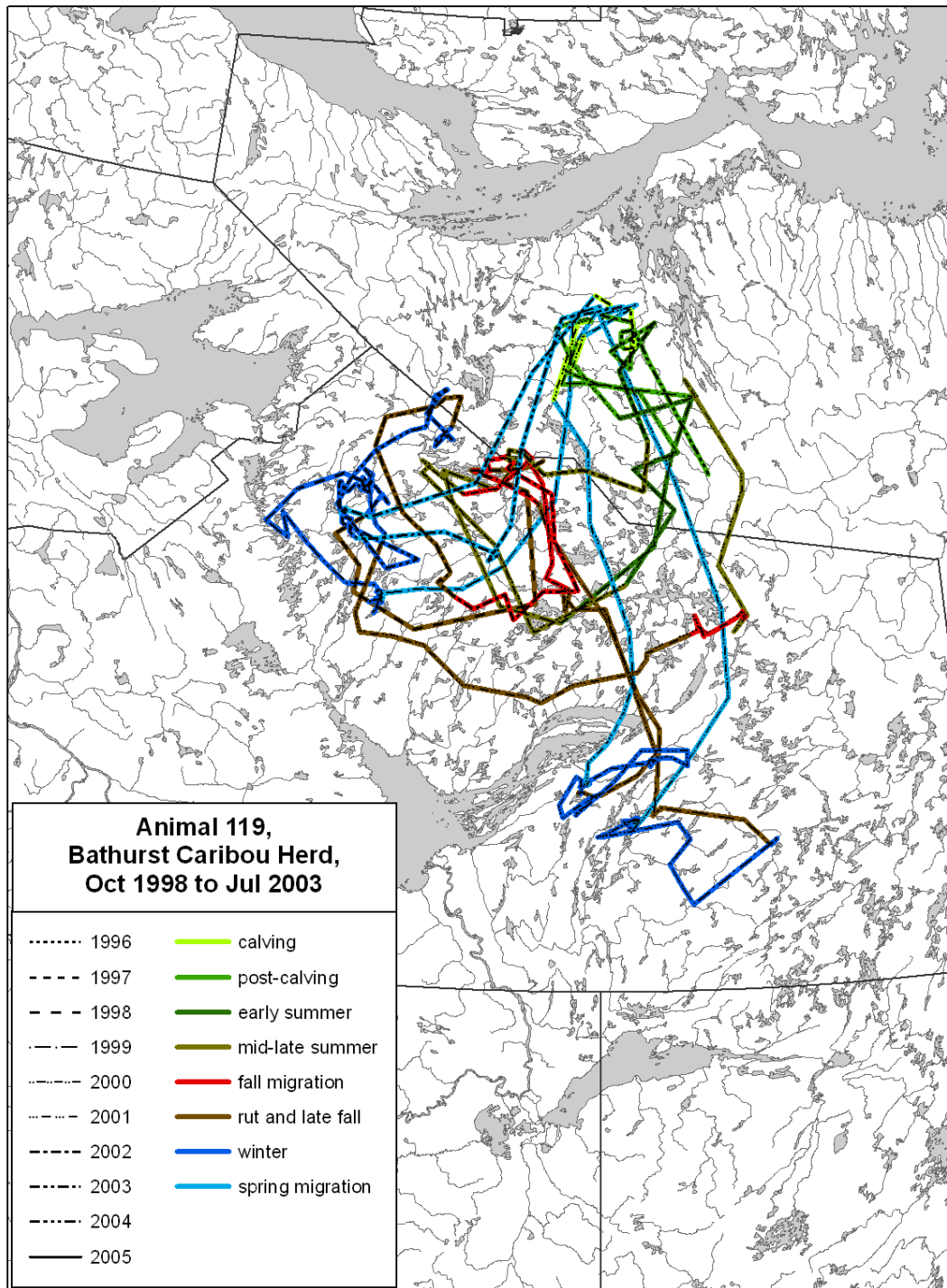


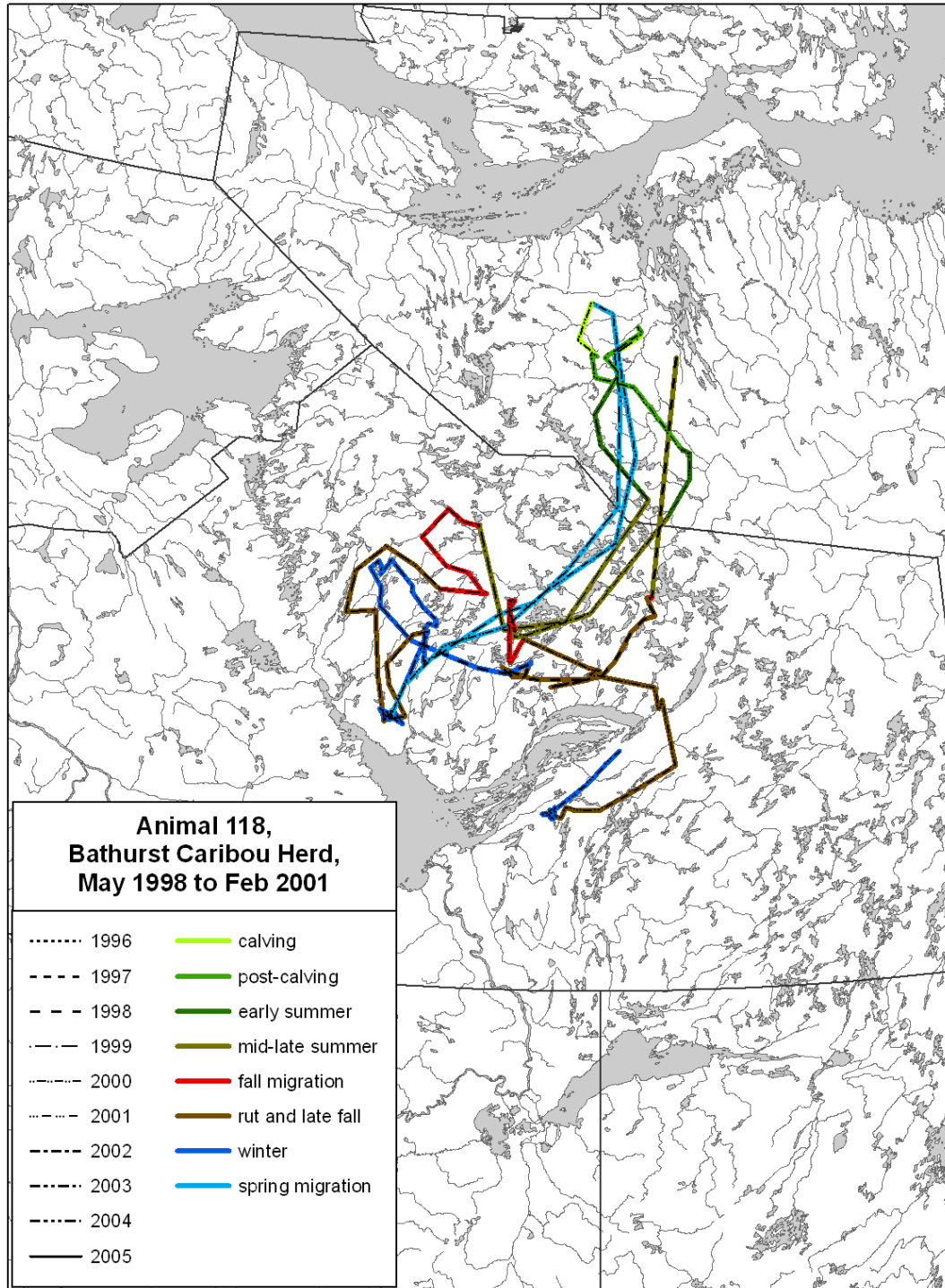


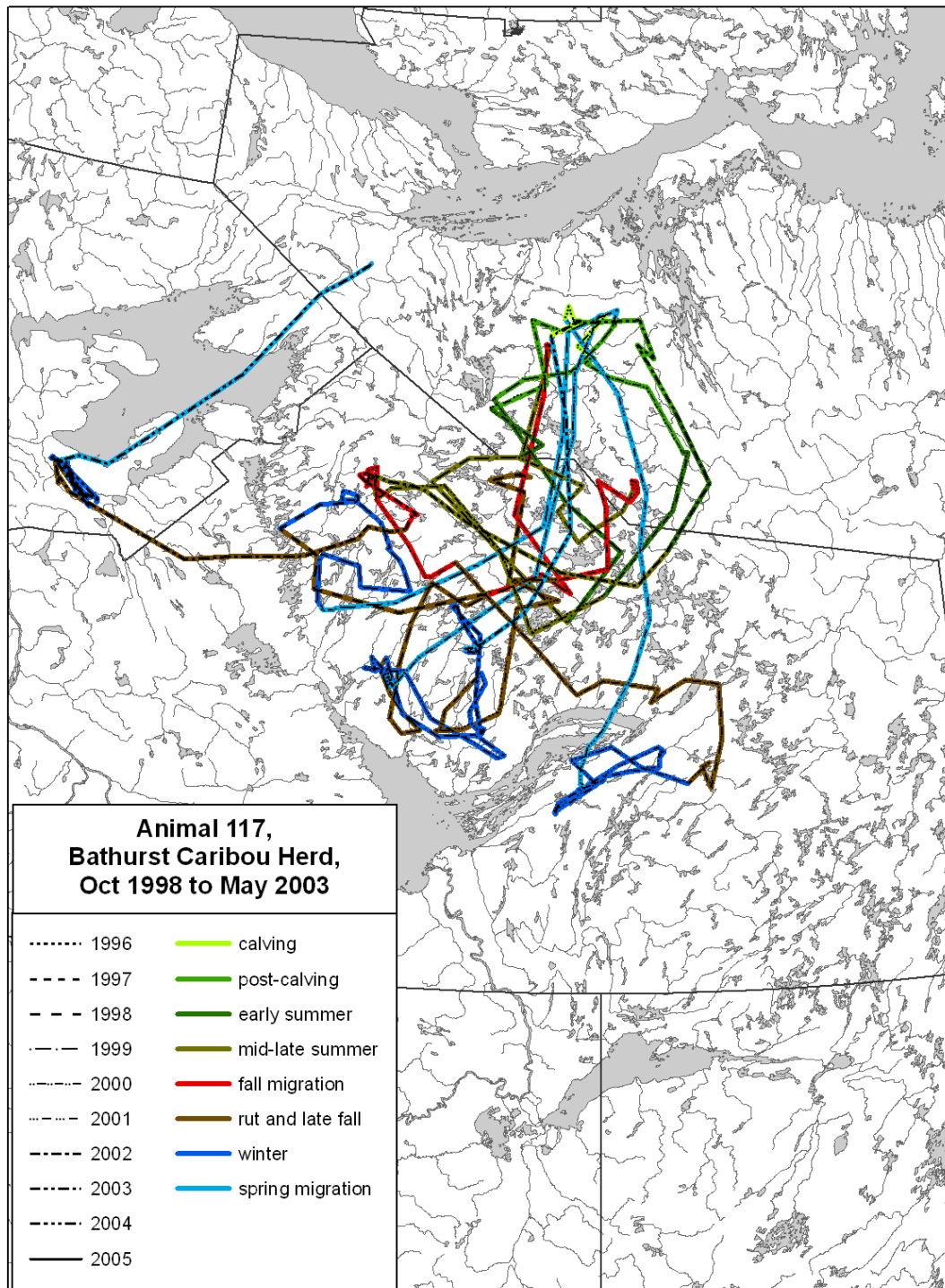


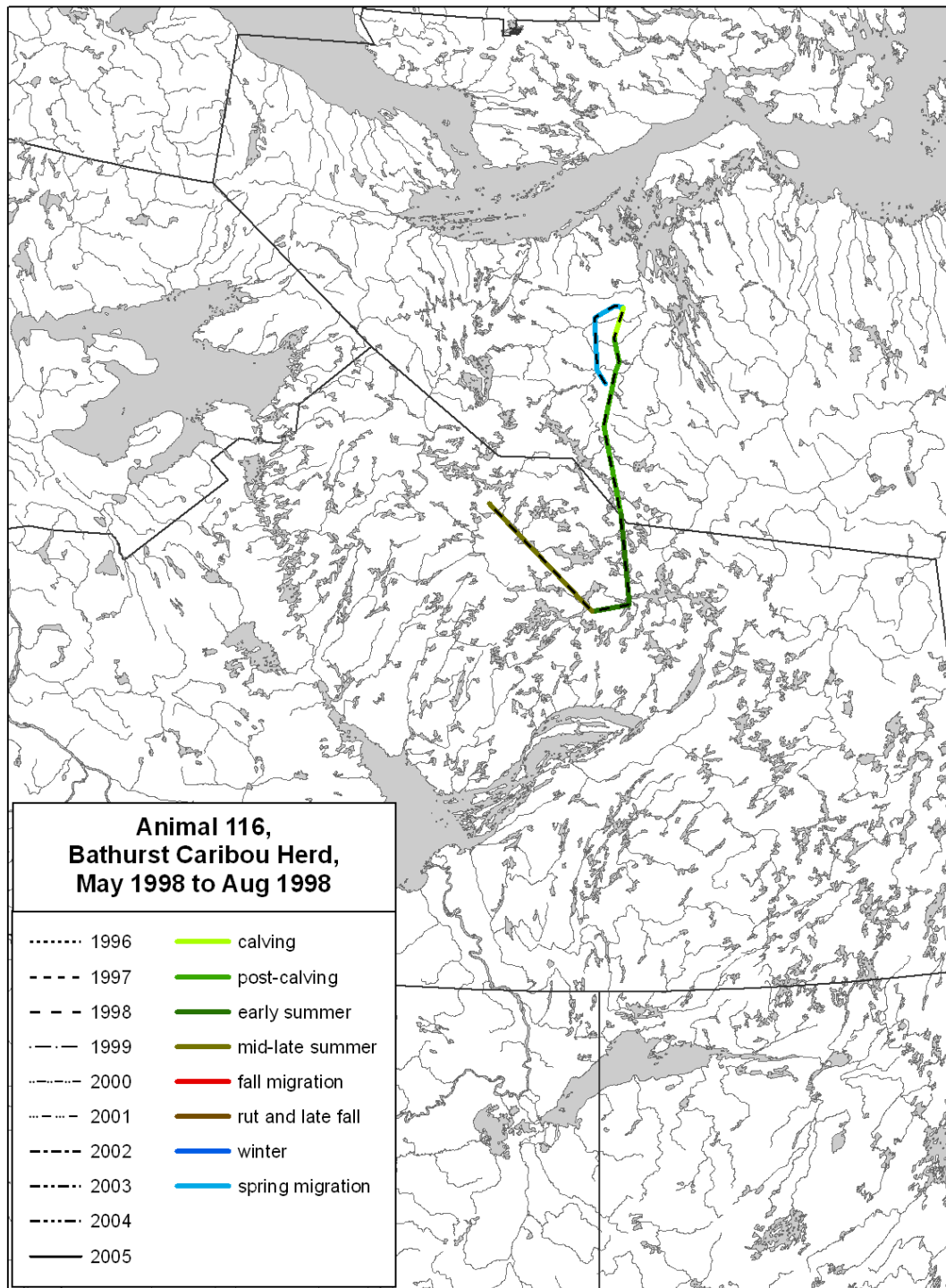


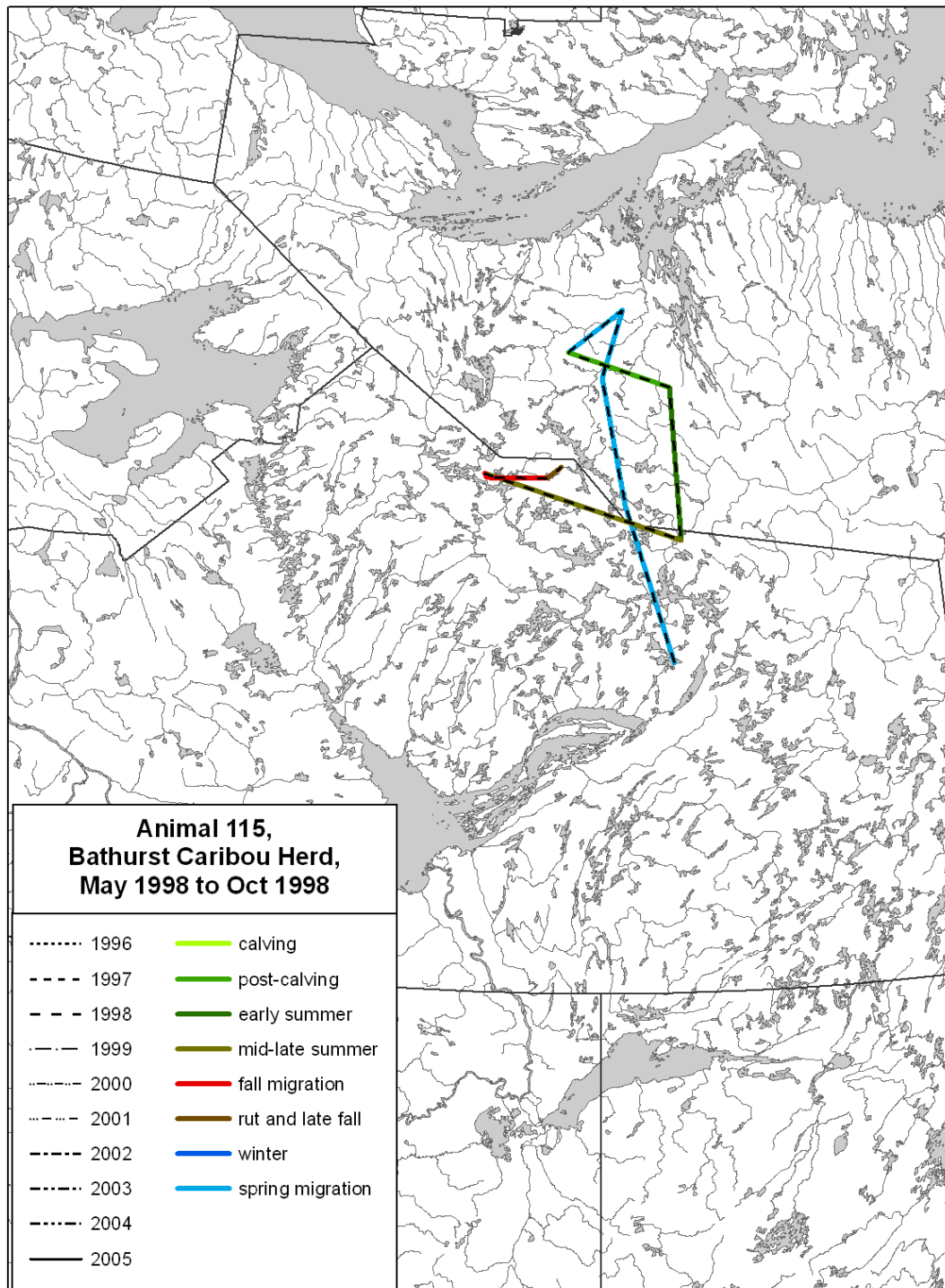


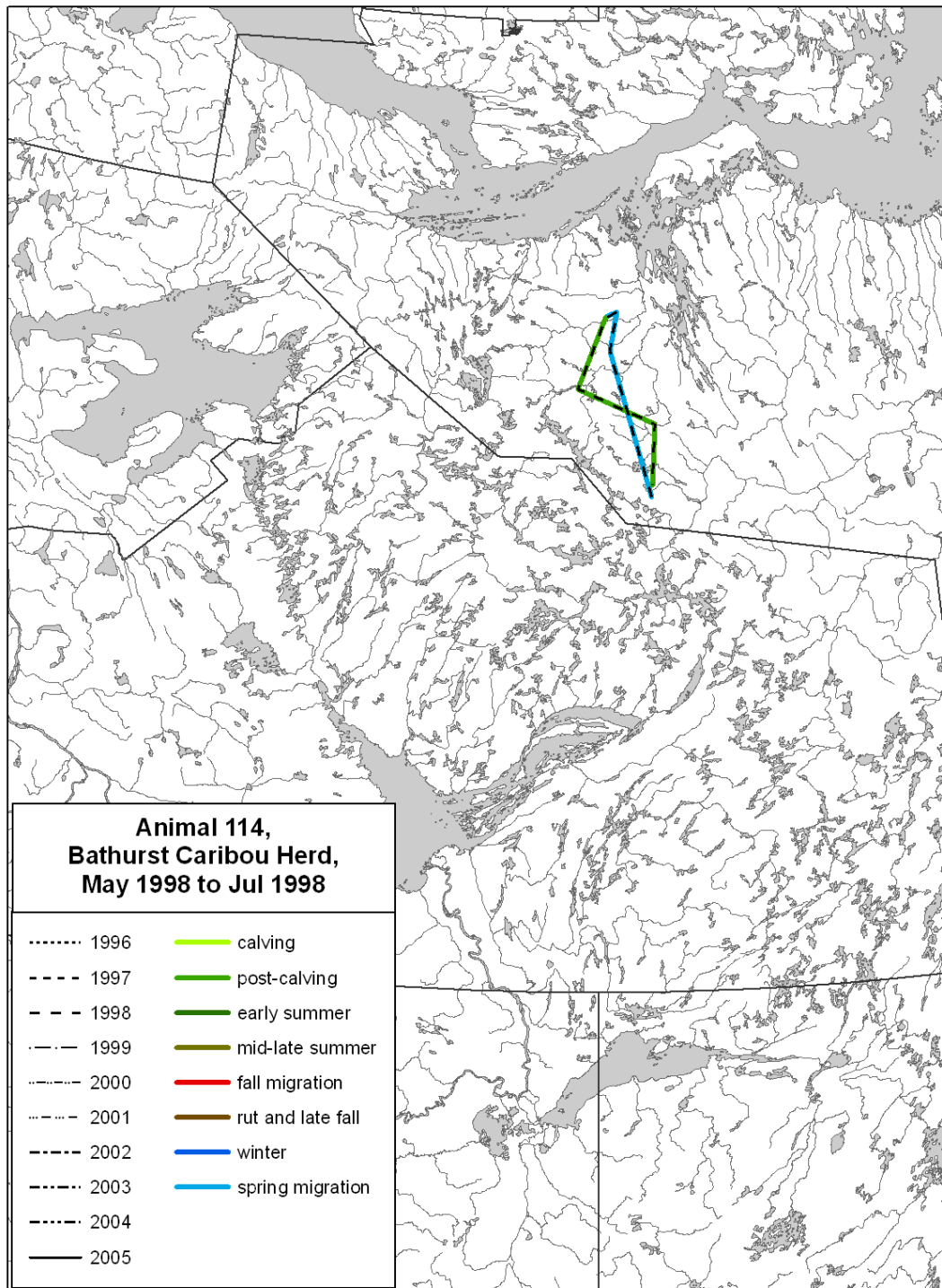


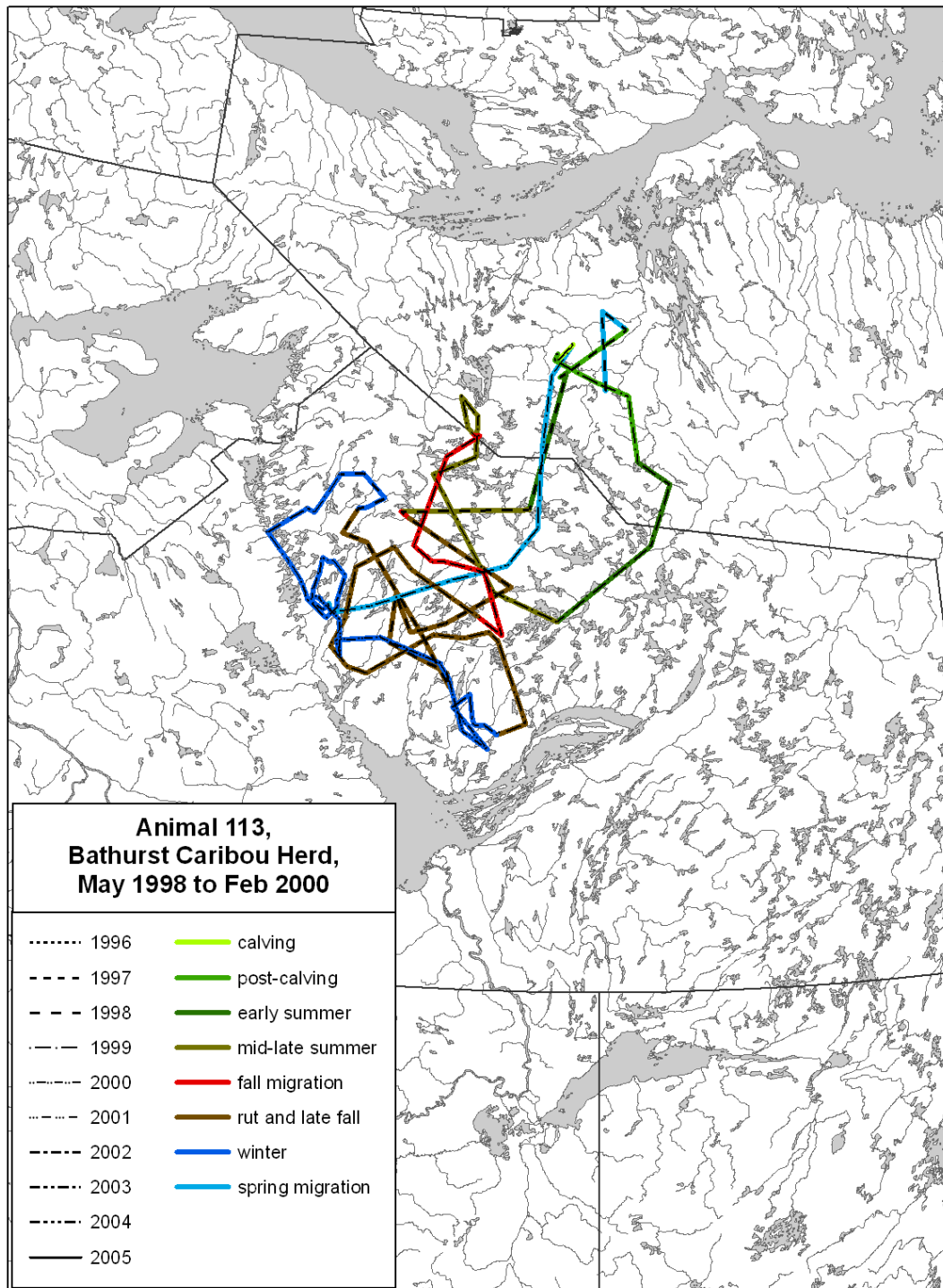


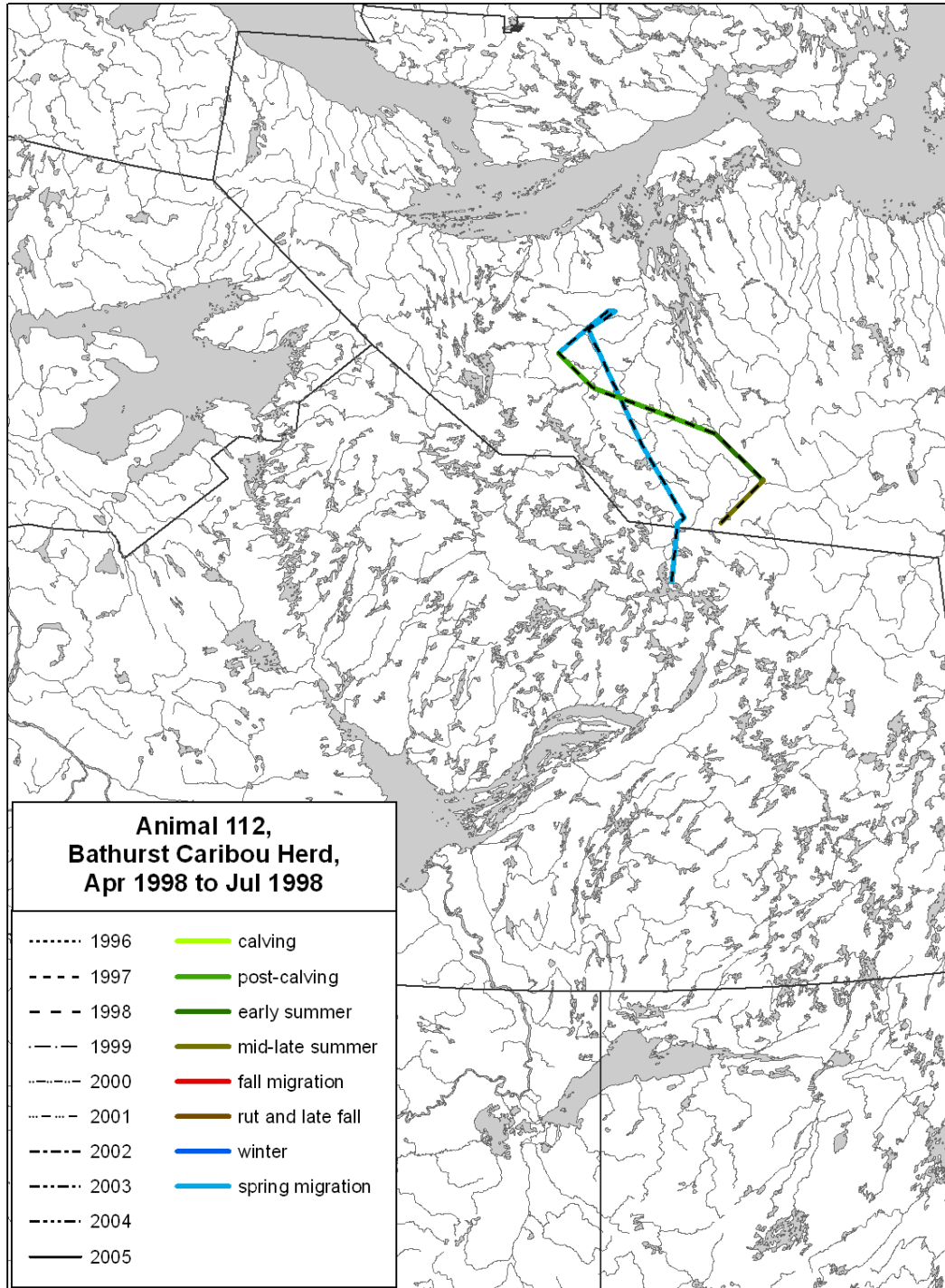


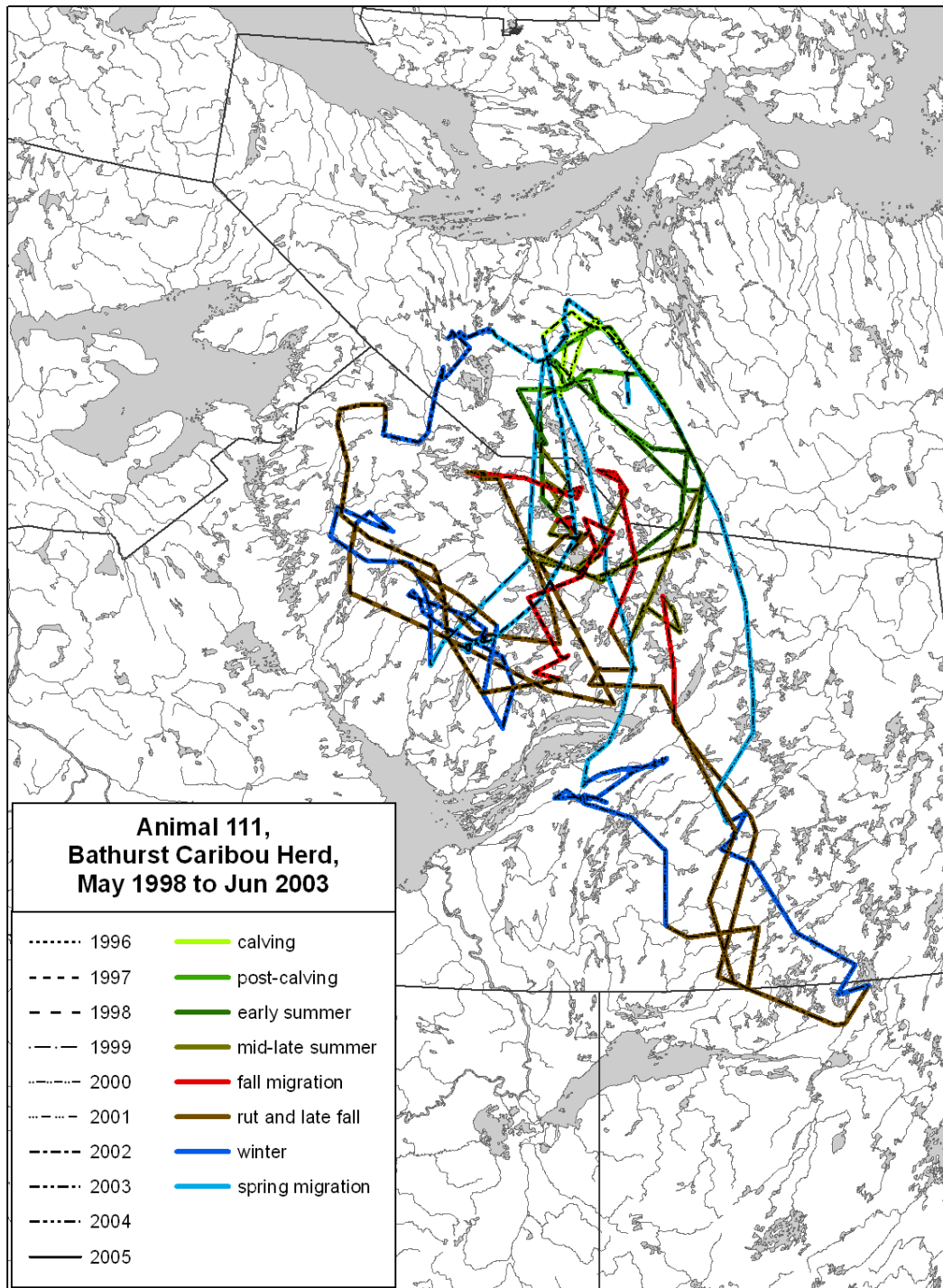


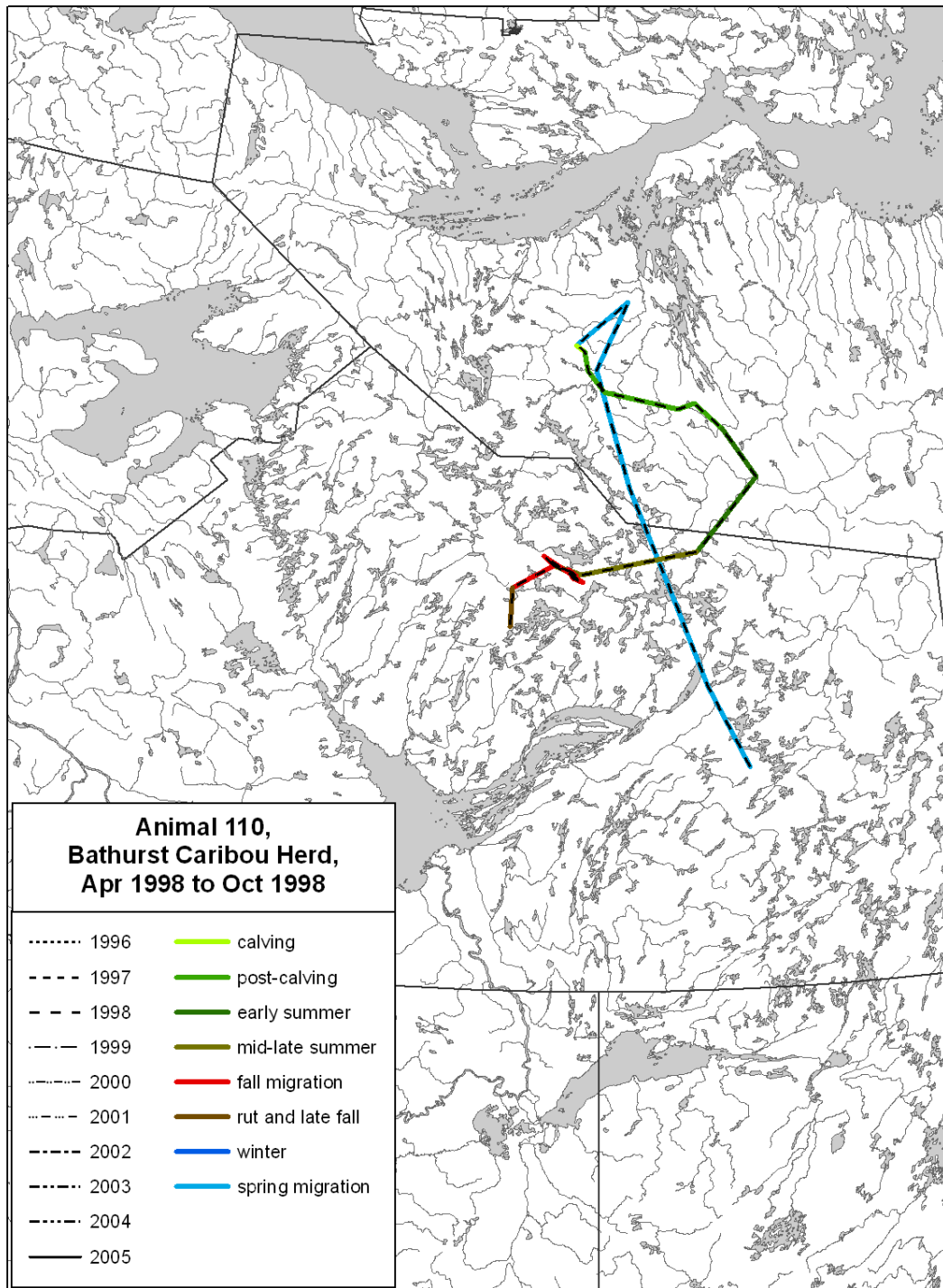


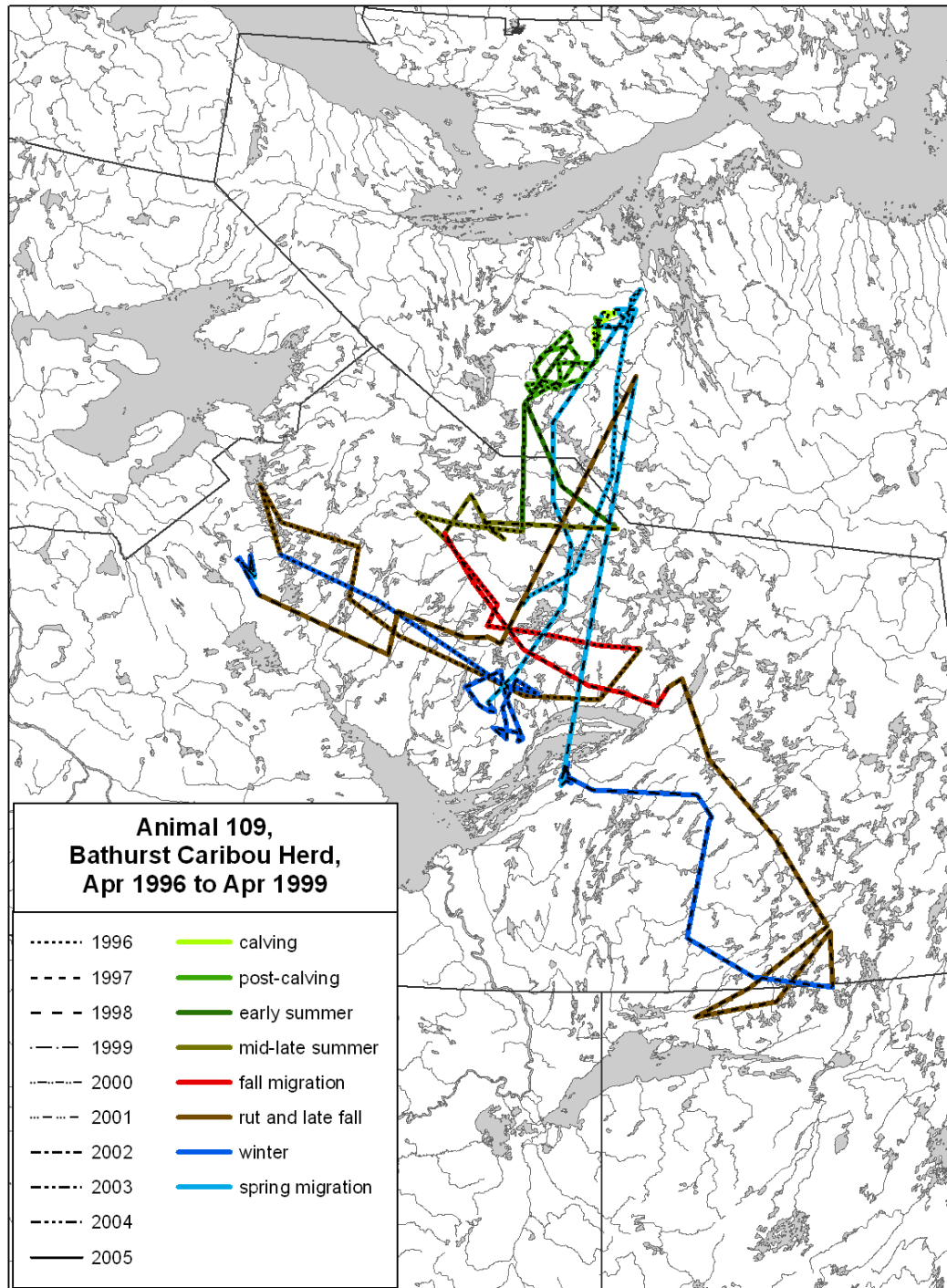


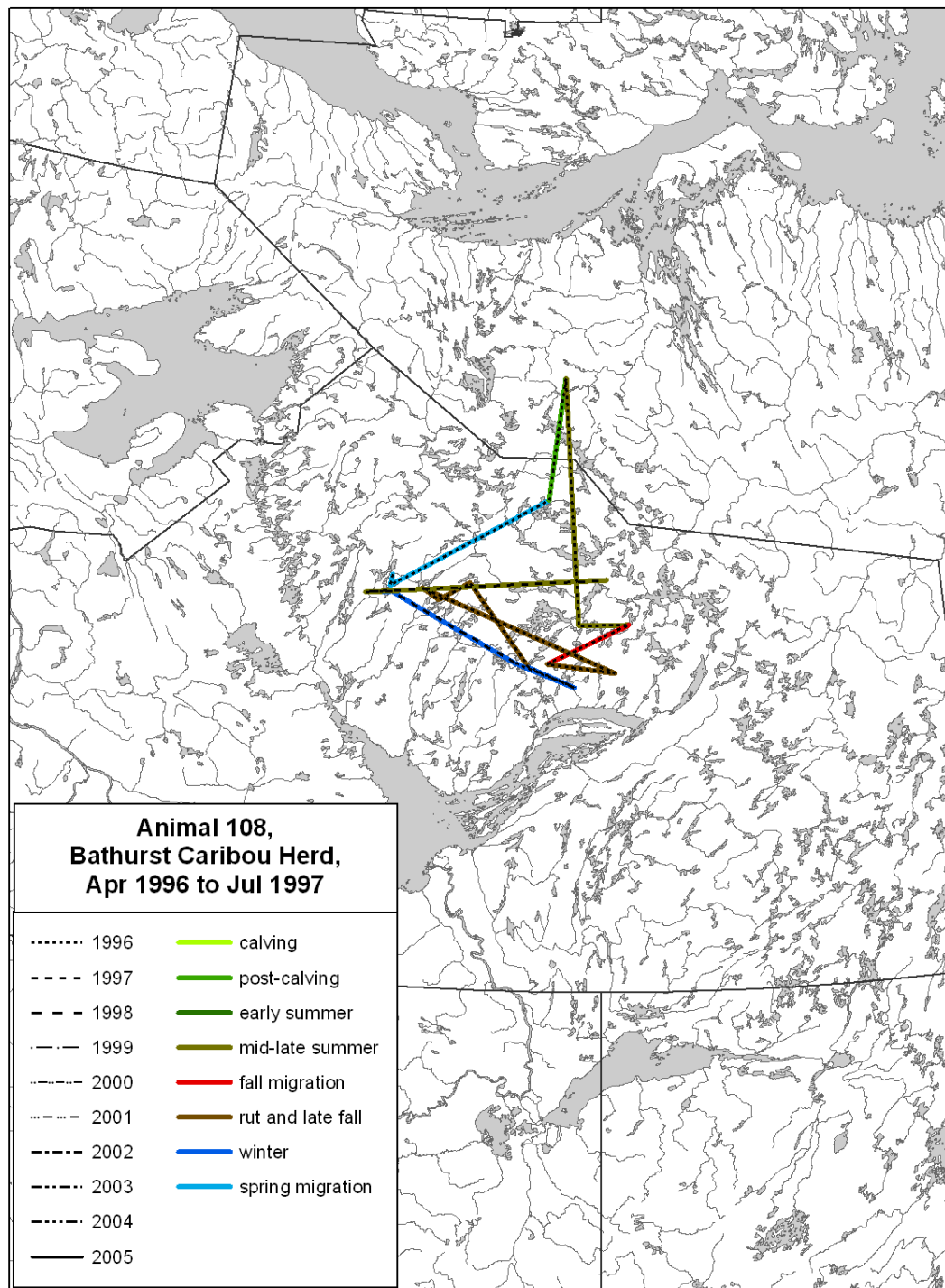


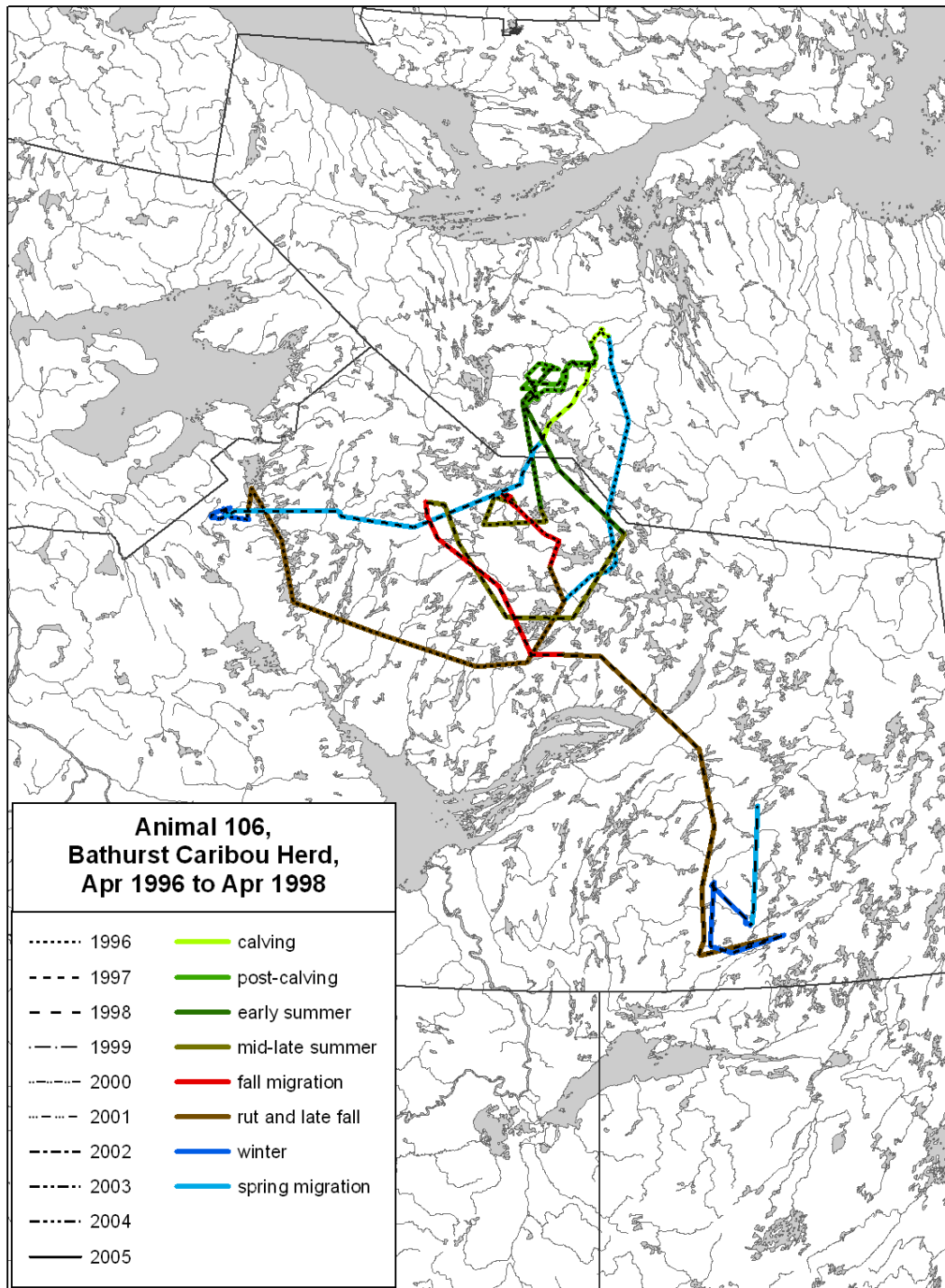


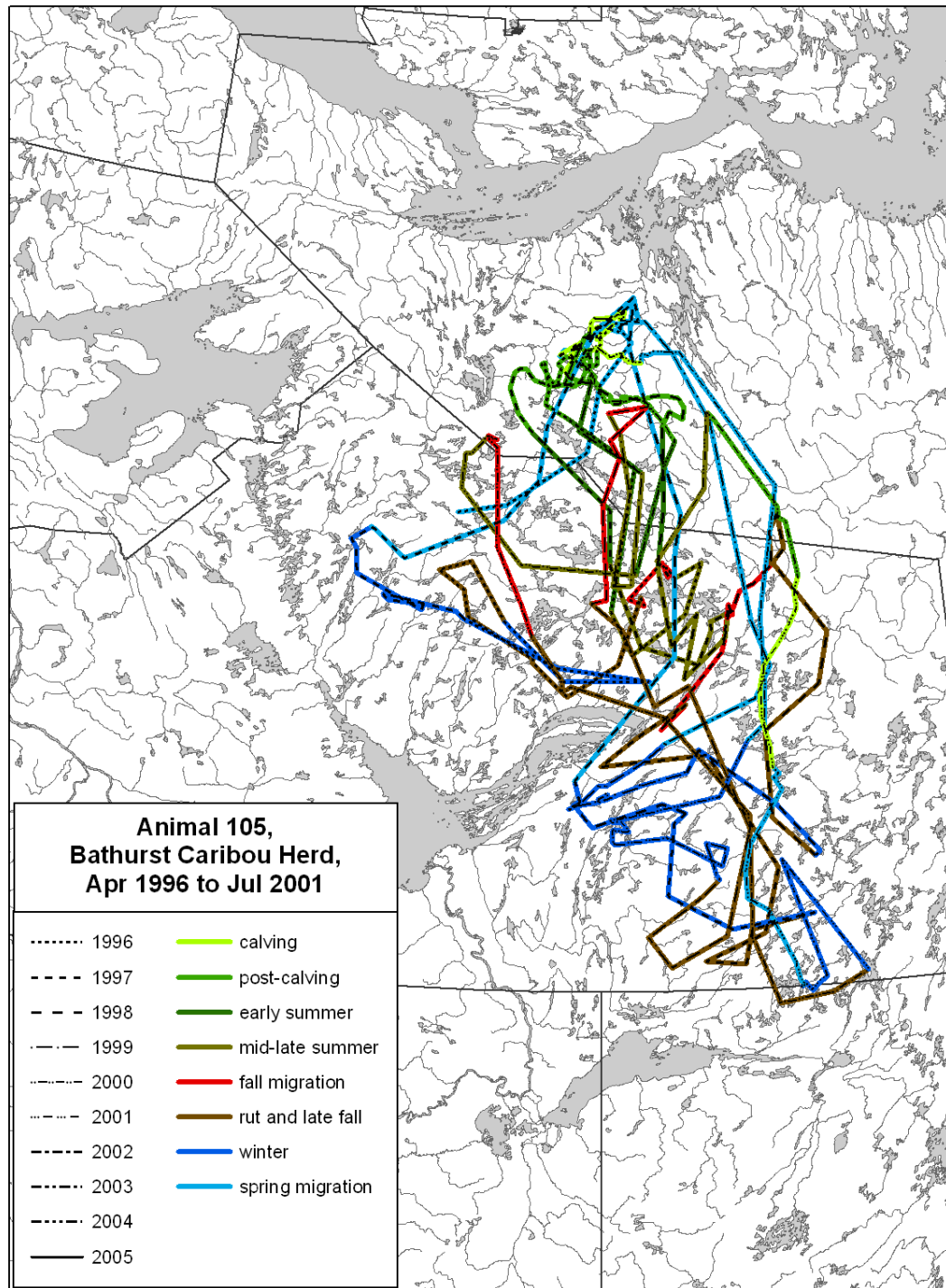


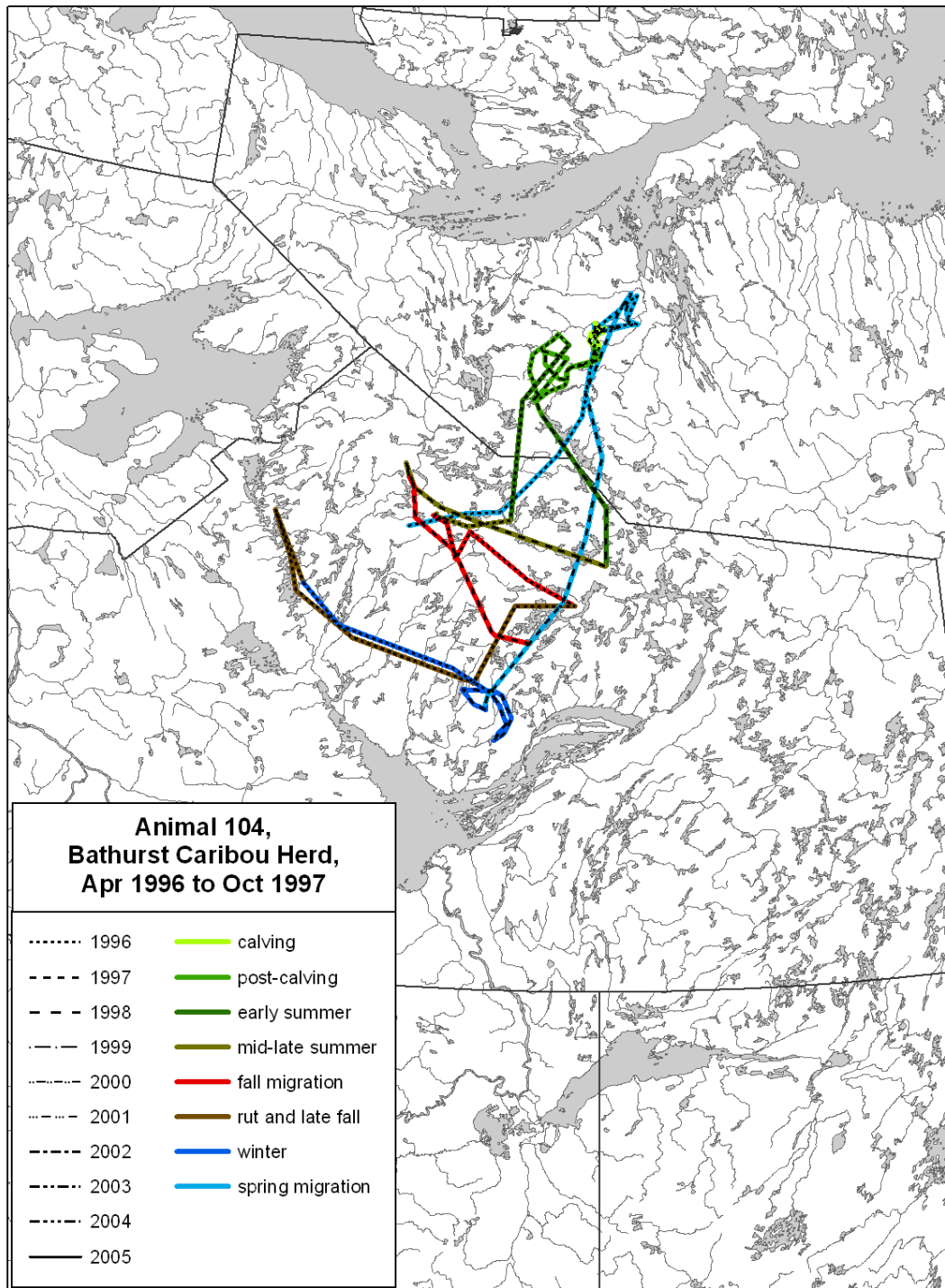


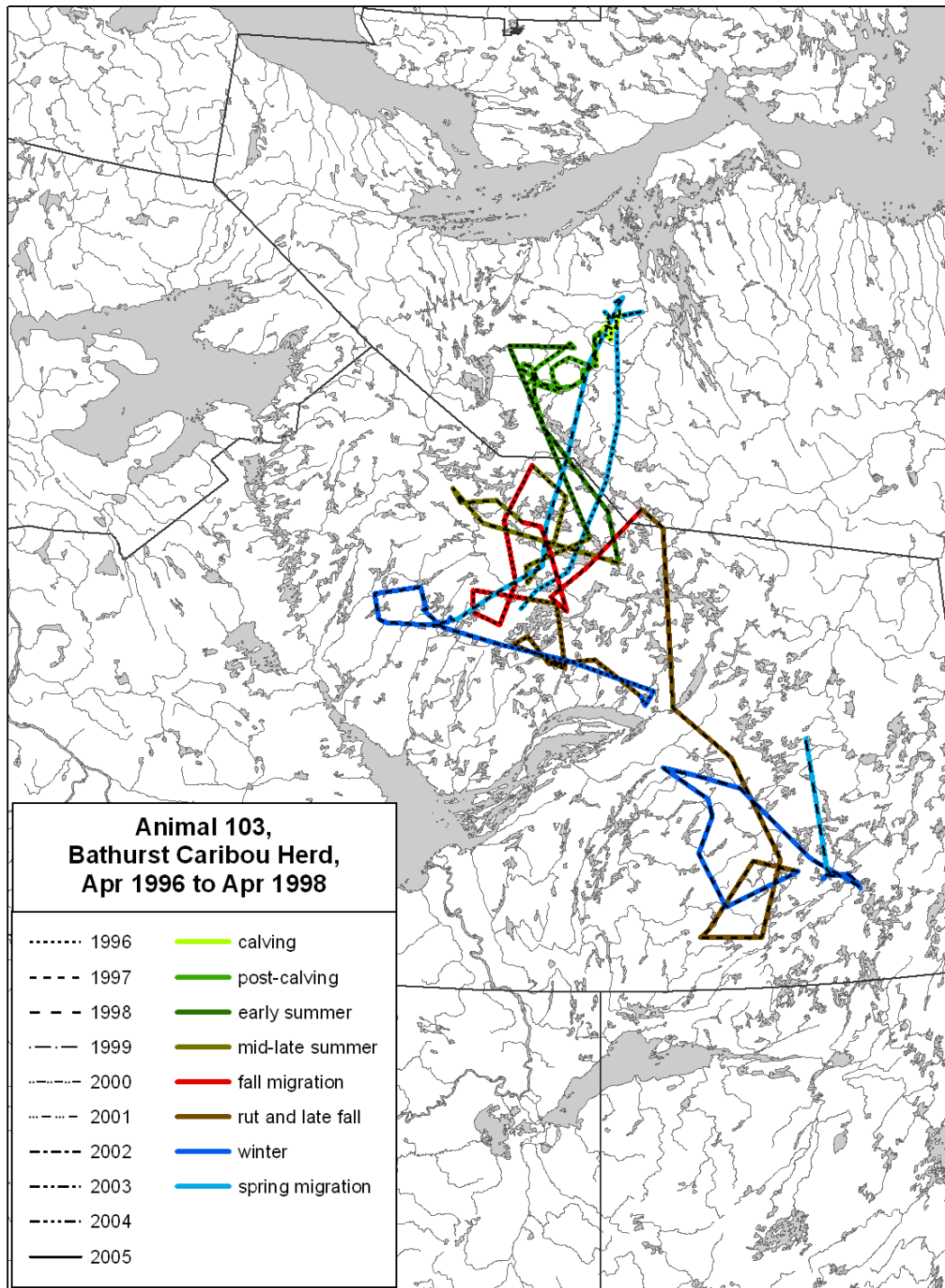


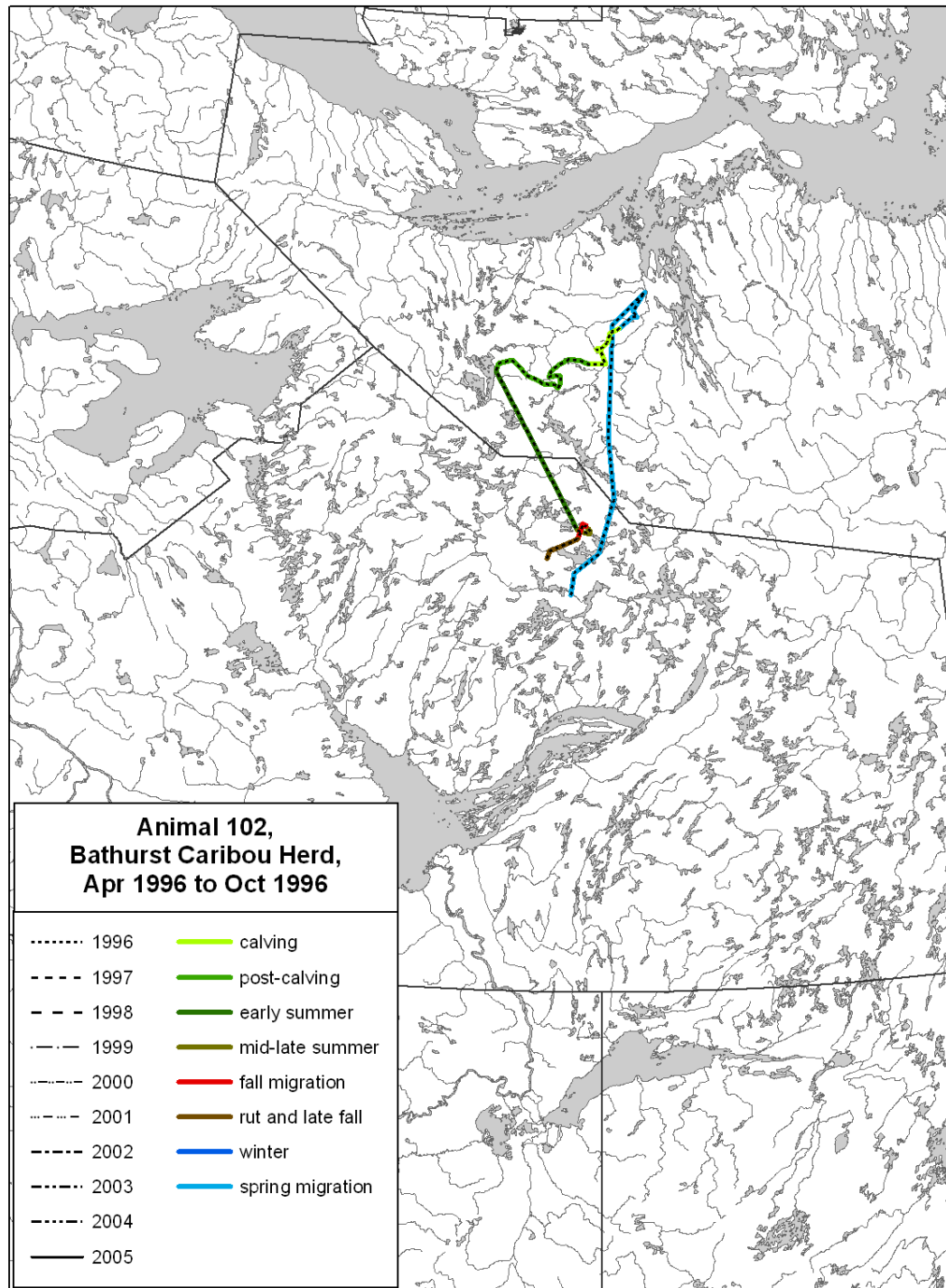


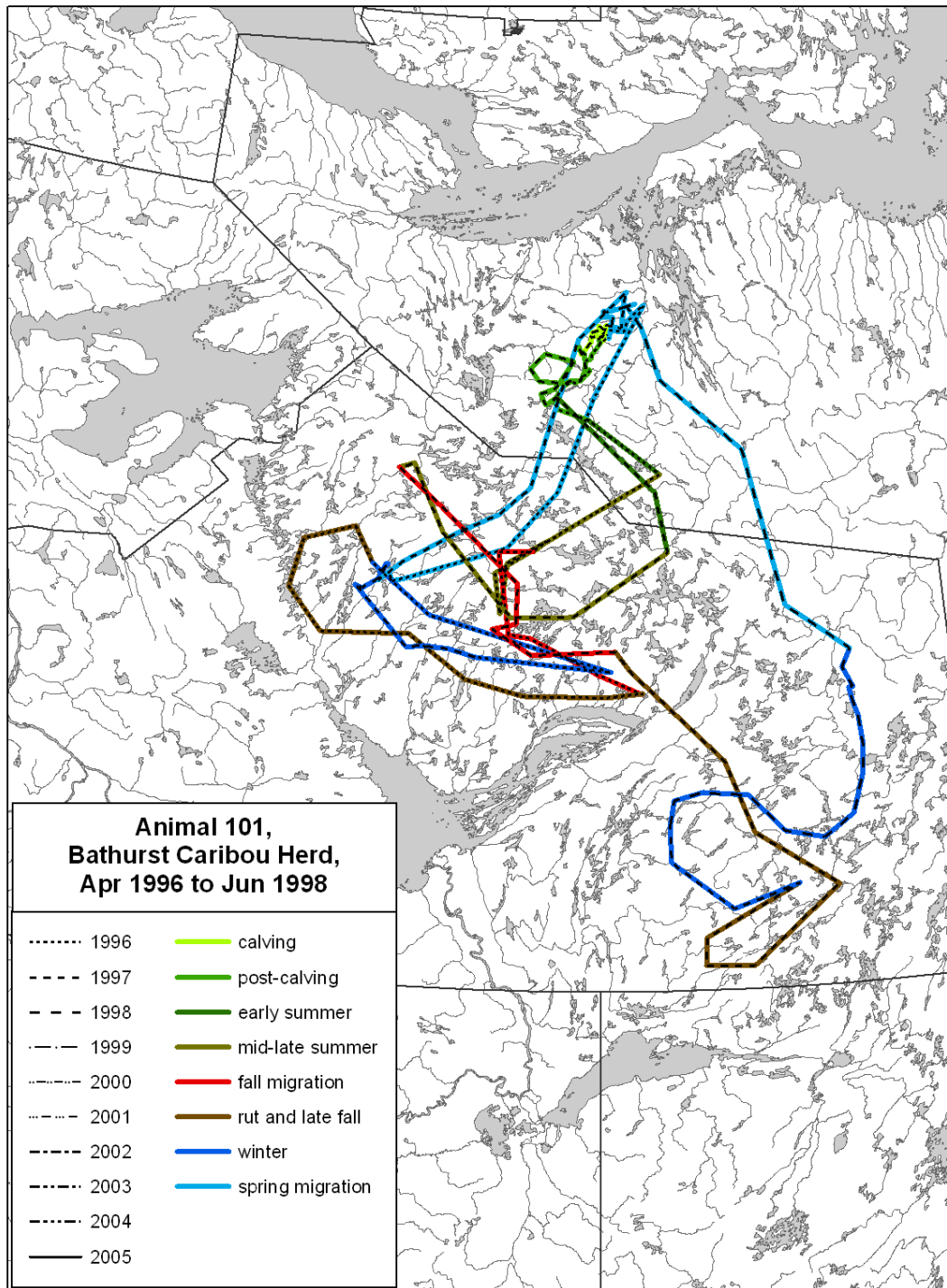


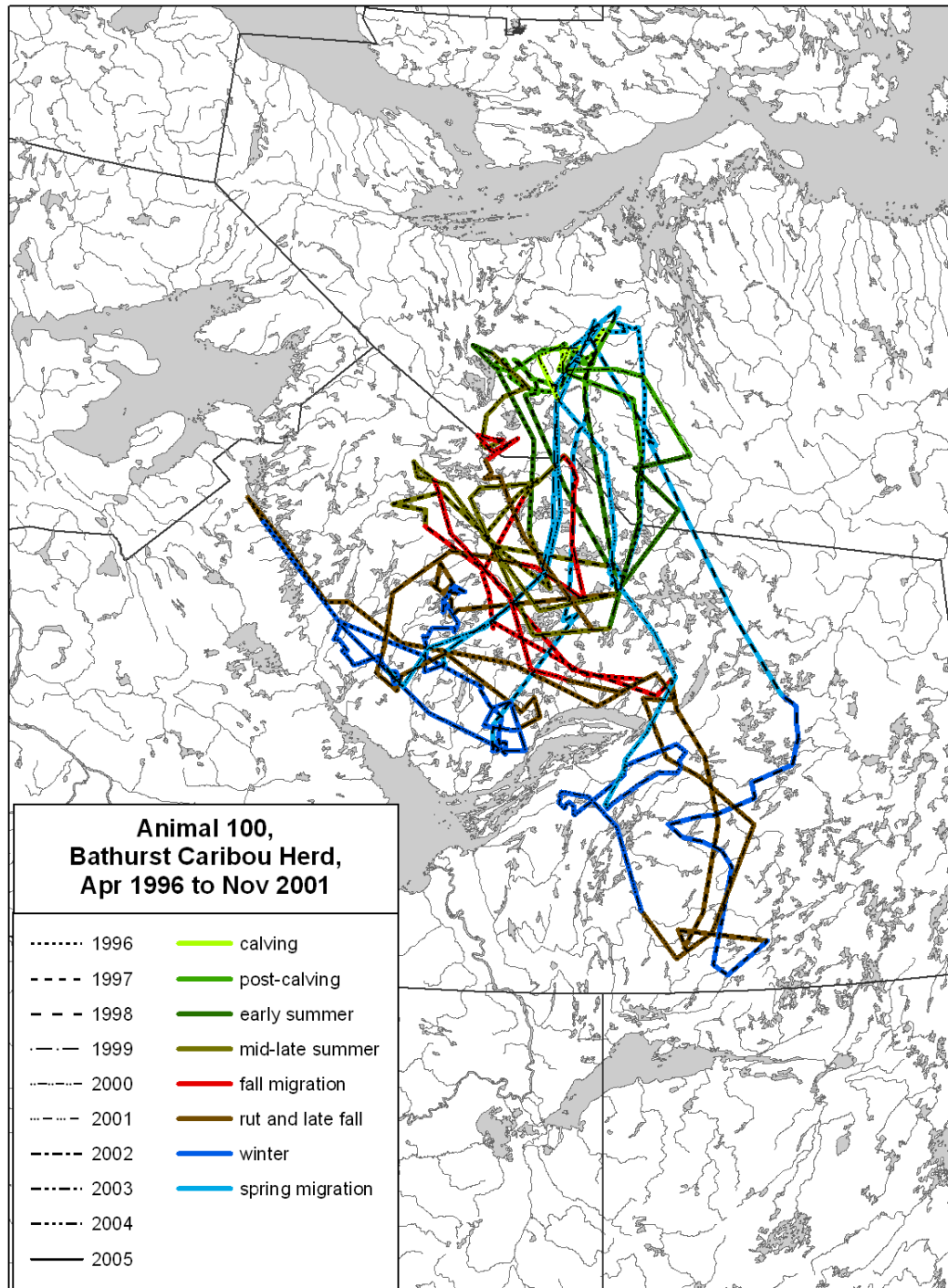












APPENDIX E: Annual maps of 3-day moving average and t-spline with 60 tension for all satellite collared cows (thick line) and individual tracks (thin lines), Bathurst caribou herd, April 1996 - May 2005

