Preliminary analysis of winter range overlaps between the Bluenose East, Bathurst and Beverly/Ahiak migratory tundra caribou herds

Contract report for

Wek'èezhìı Renewable Resources Board

by

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Executive Summary

The Bathurst herd's winter range in some years overlaps the winter ranges of its neighboring herds (Bluenose East, and Beverly/Ahiak herds). The overlapping winter distribution between the herds has complicated monitoring, assigning harvests and possibly affects potential switches of cows between calving grounds. In the 2019 Reasons for Decision report for the Bluenose East caribou herd, the Wek'èezhìi Renewable Resource Board (WRRB) noted that the lack of analyses for winter distribution which contributed to the WRRB's uncertainty about the reliability of harvest information (WRRB 2019b).

To increase understanding of the overlapping winter ranges, the WRRB initiated analyses of the caribou distribution using the Government of the Northwest Territories collared caribou. We have measured the extent of overlap at the herd and individual caribou scales which will be useful in the context of, for example, harvest and predator management and also land-use management such Caribou Mobile Measures.

We applied an index to measure the overlap and found that since 2005, the overlap between the winter distribution of the Bathurst and Beverly/Ahiak increased, especially in the most recent years. The presence and extent of the overlap between the neighboring herds varied during the 14 winters that we examined. The overlap was minimal for only 3 - 5 years for the Bathurst and Bluenose East and Bathurst and Beverly/Ahiak herds. The Bathurst herd has recently shifted its winter distribution northeast which reduced overlap with Bluenose East and increased overlap with the Beverly/Ahiak herd.

The overlap starts relatively abruptly early in winter (October) and persists through the winter until ending in May at the beginning of pre-calving migration. The overlap at the herd scale is less measurable at the scale of 200m between individual collared caribou either within a herd or across herds. The individual encounter rate was highest for the Bathurst herd which is the smallest of the three herds.

Introduction

Barren-ground caribou (*Rangifer tarandus groenlandicus*) have recently declined and are nationally classified as Threatened (COSEWIC 2016). Winter ranges contract in size and shift in location as abundance declines (Virgl et al. 2017). In recent years, shifts in the winter ranges for the Bluenose East, Bathurst and Beverly/Ahiak herds have led to overlapping winter distribution between the herds which has complicated monitoring and assigning harvests. In the 2019 Reasons for Decision report for the Bluenose East caribou herd, the Wek'èezhìi Renewable Resource Board (WRRB) noted that the lack of analyses for winter distribution contributed to the WRRB's uncertainty about the reliability of harvest information (WRRB 2019b).

The Government of the Northwest Territories (GNWT) suggested that winter overlap between neighboring herds may affect the likelihood of cows switching calving grounds as happened in 2018 and 2019 (Adamczewski et al. 2019a, WRRB 2019a). However, GNWT did not analyze trends in winter distribution, the extent of overlap and how it affected pre-calving migration. As well as being concerned about assigning harvests when neighboring herds overlap their winter

distribution, the WRRB is concerned about understanding how emigration happens because it was a factor in changes in herd sizes.

The WRRB is aware that according to many people, capturing and collaring caribou is disrespectful to caribou. This puts the WRRB in a difficult position but ensuring that the best possible use of the collar information contributing to caribou management helps to justify collaring. Over the years since in 1996, the collaring of ten cows was initiated for the Bathurst herd (Gunn et al. 2001), the number of collars has increased is why WRRB's 2019 recommended additional analyses (WRRB 2019b). Subsequently, GNWT shared the collar data with WRRB to undertake analyses of winter distribution especially the overlap between neighboring herds.

The goal of this preliminary analysis is to measure the annual extent of winter range overlap between Bathurst, Bluenose East and Beverly/Ahiak herds. We wanted to describe trends in annual overlap and chronology of when the overlap develops in winter at the herd scale. At a finer scale, the individual collared cow, we examined within and between herd spacing relative to each other as a measure of encounters. We needed to first develop quantitative indices for the overlap and encounter rate before developing analyses to describe underlying mechanisms.

Methods

1. The Caribou herds

During our study period 2005-2019, the Bluenose East, Bathurst and Beverly/Ahiak herds were declining. WRRB (2019a) summarizes the technical and community evidence for the Bathurst and Bluenose East herds. The Bathurst herd declined from a 1986 peak of 470,000 to an estimate of 19,800 in 2015 and then the decline accelerated to approximately 29% a year to 8,207 in 2018 (WRRB 2016 and 2019a). The Bluenose East herd has declined 81% since the 2010 estimate of 103,000 relative to the 2018 estimate of 19,300 caribou (WRRB 2019b).

Changes in calving distribution in the 2000s and differences in their interpretation have complicated describing declines in the Beverly/Ahiak herd (COSEWIC 2016). Campbell et al. (2019) report that the Beverly/Ahiak herd declined from 136,600 in 2011 to 106,000 estimated in 2018.

2. Data

We used GNWT's caribou collar data that GNWT uploaded to the Movebank repository (http://movebank.org, accessed Feb 2020). The data are organized in "studies", and the full names of the three specific studies we downloaded are: *ABoVE: NWT Sahtu Barren Ground Caribou: Bluenose-East*, *ABoVE: NWT North Slave Barren Ground Caribou: Bathurst* and *ABoVE: NWT South Slave Barren Ground Caribou: Beverly and Ahiak*. These datasets include nearly 1 million locations collected from 747 individuals (Table 1, spring 1995 to fall 2019).

To clarify the herd assignments in the raw data, we performed a cluster analysis on all the caribou average (1 -3- June calving location and separated the animals into three herds of interest (Bluenose East, Bathurst and Beverly/Ahiak; Appendix B). After removing those animals that

belonged to other herds or remained unclassified, the resulting dataset contains 619 individuals (176 F and 70 M from Bluenose East, 153 F / 37 M for Bathurst, and 151 F / 32 M for Beverly/Ahiak). The duration varied (Figure 1) and the average durations were about 576 days of observation (inter-quartile range: 276-938).
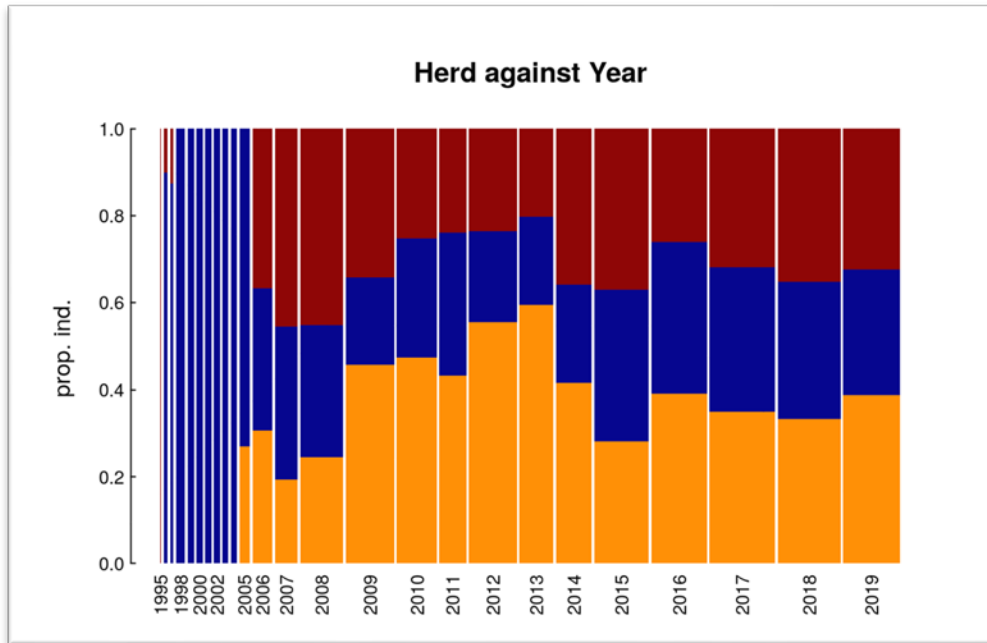
Figure 1 Barplot of relative number of collared caribou and the proportion of individuals across years and three herds. Widths of bars are proportional to the total number of collared individuals in a given year. Blue-Bathurst; yellow = Bluenose East and Red= Beverly/Ahiak

Table 1. Sample size of satellite or GPS collared male and female caribou by herd and year.

	Bluenose East	**Bathurst**	**Beverly and Ahiak**
1995	0	0	1
1996	0	9	1
1997	0	7	1
1998	0	22	0
1999	0	15	0
2000	0	15	0
2001	0	15	0
2002	0	15	0
2003	0	14	0
2004	0	14	0
2005	7	19	0
2006	15	16	18
2007	11	20	26
2008	26	32	48
2009	55	24	41
2010	47	27	25
2011	29	22	16
2012	66	25	28
2013	50	17	17
2014	37	20	32
2015	38	47	50
2016	54	48	36
2017	57	54	52
2018	52	49	55
2019	55	41	46

3. Analyses

Fieberg and Kochanny (2005) comprehensively reviewed overlap indices for wildlife data, and recommended indices which are "appropriate" (i.e., consistent with one's intuition of overlap) and "simple" (i.e., easy to interpret), while also taking into account differences in the relative probability of space-use throughout estimated utilization distributions (UD's).

To that end, we select the *Volume of Intersection Statistic* (VI) which is defined as $VI = \int_A \min\left(UD_i, UD_j\right) dA$, where the UD is a probability distribution of finding an animal at a given point, estimated using bivariate normal kernels (Benhamou and Cornelis, 2010). The VI is a symmetric index ranging from 0 to 1 that captures the shared *volume* of the overlap of the kernel densities - two identical distributions have 100% overlap; two completely separated distributions have 0% overlap (Figure 2). An important weakness of this method is that there are some unpredictable biases that emerge from the estimation of the UD itself (Fieberg and Kochanny 2005), especially if the movement data are highly autocorrelated (Fleming et al. 2015).

Nonetheless, these indices are straightforward methods to characterize the general proximity and shared space used by individuals or groups of individuals.
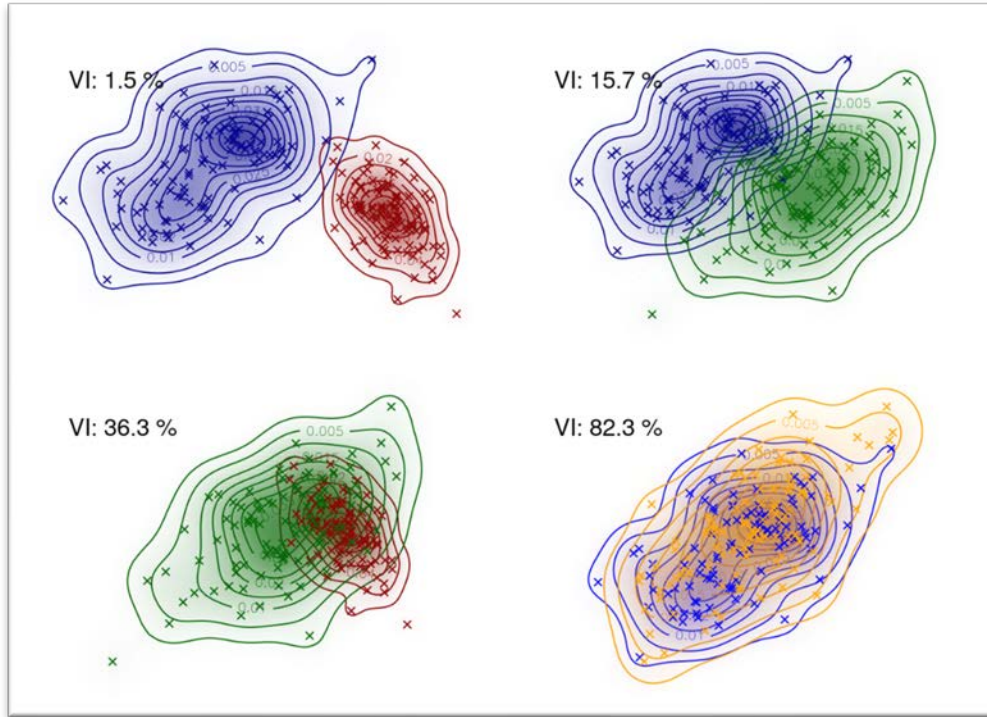
Figure 2. Various levels of volume intersection (VI) overlap index for four different pairs of simulated data. The "x"s represent 100 simulated locations for each colored (blue, red, green, orange) populations and the shaded areas and contour lines represent the estimated utilization distribution (UD) . In the last (bottom right) example, with the highest overlap, the two samples were drawn from the same underlying distribution.

We computed VI indices for each year across herds and across individuals during a winter period defined as November 1 - April 1, i.e. after the completion of the fall migration and before the beginning of the spring migration. We addressed possible bias from the time interval for locations (Appendix A). To look more closely at the seasonal dynamics of overlap, we also looked at inter-herd overlaps across the year. To do this, we blocked the year into 6-day intervals and took location data from every other day of observation within the block (i.e. day 2,4,6) to control for autocorrelation. This allowed us to explore more closely the rate at which overlap increased from near zero (as expected during calving) to the higher numbers observed in several of the winter seasons.

Although we used fixed seasons, we also wanted to be able to describe the timing of fall migration including the rut so as to be able to describe the beginning of winter distribution for the three herds. We used a proximity analysis to describe a more detailed, and alternative look at inter-individual distances to estimate an encounter rate. We counted the number of individuals within a given set of distance thresholds (200, 100 and 50 m) on a given day. The pairwise distances

between collared individuals as a metric of social interaction and grouping. We examined pairwise distances within herds (intra-herd) and across herds (inter-herd).

Results

1. Intra- and Inter-herd Overlaps
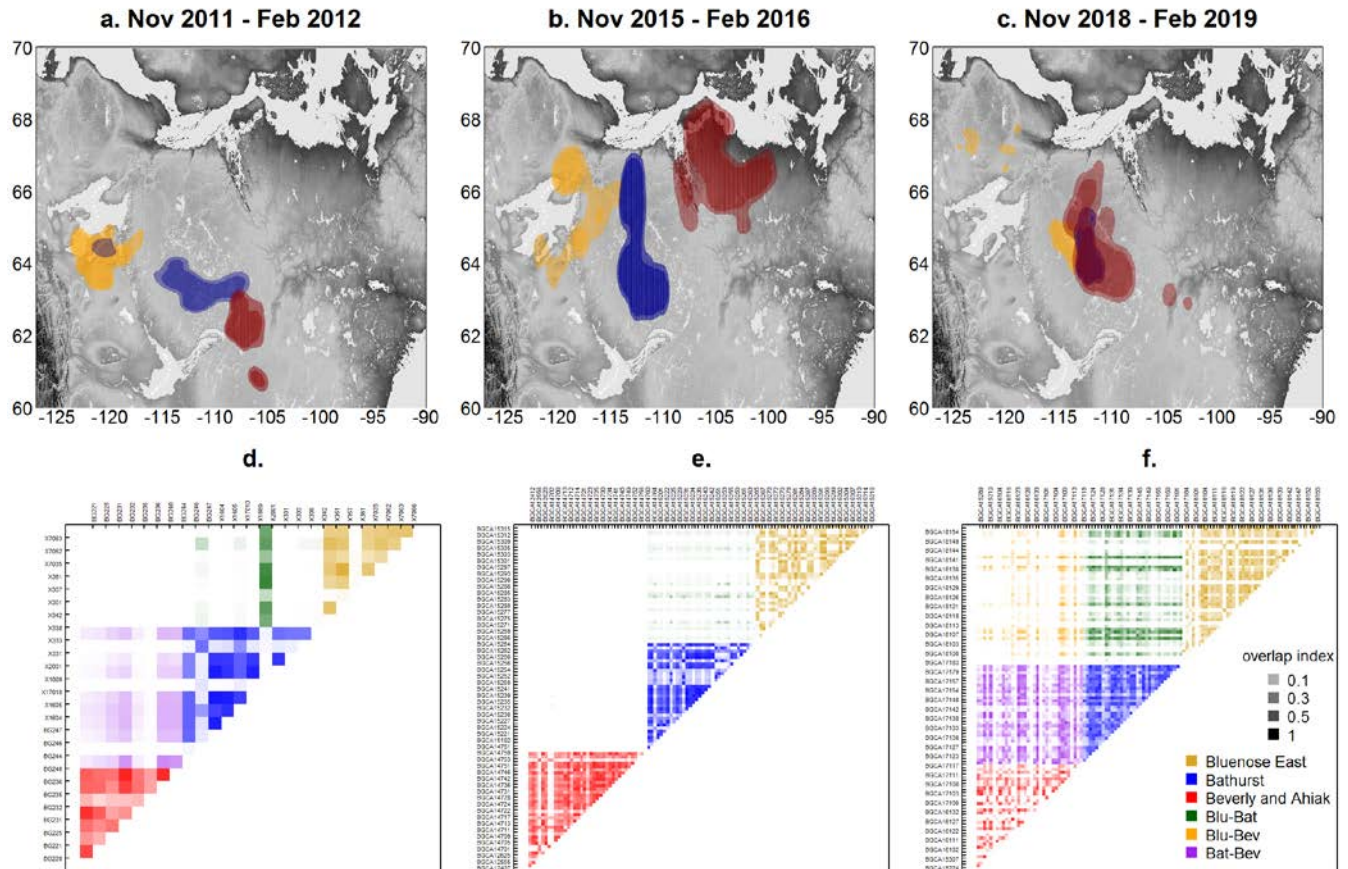
Figure 3. Top panels - estimated winter (November 1 - Feb 28) utilization distributions (UD) in three well-contrasted years (left to right: 2011-12, 2015-16, 2018-19), Bluenose East, Bathurst and Beverly/Ahiak animals in yellow, blue and red, respectively. Lower panels - individual overlap matrices, where each square indicates a single overlap value across individuals. Within-herd overlaps are in yellow, blue and red, as above, while intra-herd overlaps are in off-diagonal blocks in mixed colors. Darker squares indicate higher overlap. For example, in 2011-12 individual X1899 of the Bathurst herd overwintered among Bluenose East animals as evident from the green vertical bar – the only significant cross-herd interaction. In contrast, in 2018-19, there was considerably cross-herd overlap among individuals.

As an initial step, we mapped the winter distributions as utilization distributions since 1997 for the Bathurst herd with the overlap with neighboring herds which is available as a separate file (Appendix C). Using three well-contrasted winters (2011-12, 2015-16, 2018-19), we summarize the overlaps across herds as individual collared caribou overlap matrices (Figure 3). The variation

in latitude (southernmost in 2011-12, northernmost in 2015-16) is wide and suggests a trend in the Bathurst herd's winter distribution shifting north.

The median overall overlap was highest for Bluenose-East-Bathurst compared to the Bathurst-Bluenose East overlap and Bluenose East-Beverly/Ahia overlap (Table 2). The overlap is annually variable e.g. in 2011-12, Bluenose-Bathurst and Bathurst-Beverly overlap 3.5% and 5.5%, respective, compare to 27% and 52% in 2018-19 (Table 3, Figure 3). The trends, as measured by a linear regression for the overlap between the Bathurst and its two neighboring herds, changed over the period 2005-2018 with the Bathurst-Bluenose East decreasing (r^2=0.19) and Bathurst-Beverly/Ahiak increasing (r^2=0.34).

Table 2. Median and 25% and 75% Quartiles for overall overlap between neighboring herds.

Herd 1	Herd 2	Median	Q25	Q75	Min	Max
Bathurst	**Bluenose East**	25.5	11.5	38.8	0.0	46.1
Bathurst	**Beverly/Ahiak**	18.5	7.9	25.8	0.2	63.2
Beverly/Ahiak	**Bluenose East**	3.1	0.1	4.3	0.0	25.0

Table 3. Estimated mean Volume of Intersection Statistic (VI) overlap for the pairwise comparisons for the Bluenose East, Bathurst and Beverly Ahiak herds 2005-2019.

Winter	Bluenose East – Bathurst	Bathurst – Beverly/Ahiak	Bluenose East – Beverly/Ahiak
2005-06	2.0	NA	NA
2006-07	31.1	3.7	18.5
2007-08	28.3	0.0	19.3
2008-09	37.1	0.1	4.8
2009-10	44.0	5.2	10.1
2010-11	41.0	0.0	0.1
2011-12	11.8	0.0	7.1
2012-13	28.0	3.6	13.7
2013-14	6.9	3.2	12.9
2014-15	11.9	1.9	4.5
2015-16	5.5	0.2	3.5
2016-17	43.4	7.5	31.1
2017-18	0.0	0.1	63.6
2018-19	27.9	25.1	51.6

2. Seasonal dynamics of herd overlap

To explore in more detail the seasonal dynamics of herd overlap, we further computed the VI index across herds on a fine 5-day scale from the beginning of 2006 (Figures 4, 5 and 6).
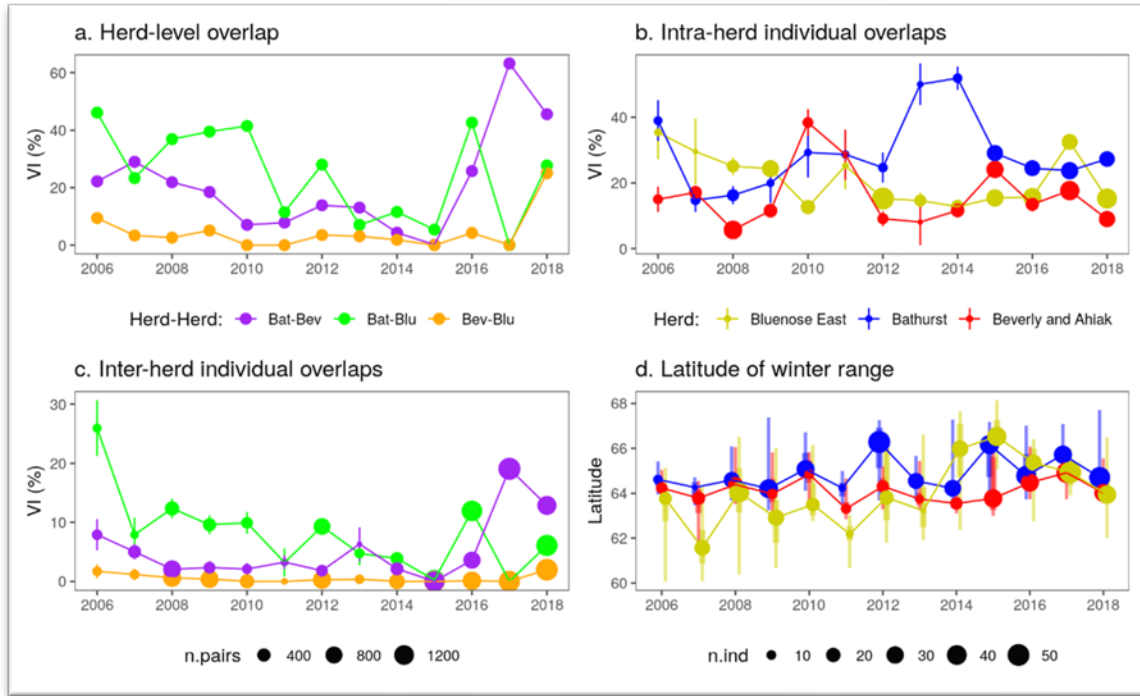
Figure 4. Estimated VI overlap at (a) herd level, (b) among individuals within a herd and (c) among individuals across herds. Vertical bars in (b) and (c) indicate 95% standard error around the means, and size of circles represents number of pairs. Panel (d) shows the median (circle), inter-quartile range (thick line), and inner 95% quantile range (thin line) of the latitudes of the winter ranges across time, with the size of the circle proportional to the number of individuals.

The VI overlap varied across years: generally, the overlap was higher in the years 2006-2010 across the herds compared to 2011-2018. With the exception of 2007 and in the most recent years, winter overlap was generally higher between Bluenose East and Bathurst herds (Blu-Bat) than between Bathurst and Beverly/Ahiak (Bat-Bev). Bluenose East - Beverly/Ahiak (Blu-Bev) overlap was - as expected - lowest overall (median 0.0015, inter-quartile range: 0-0.027), and essentially zero in the calving months.
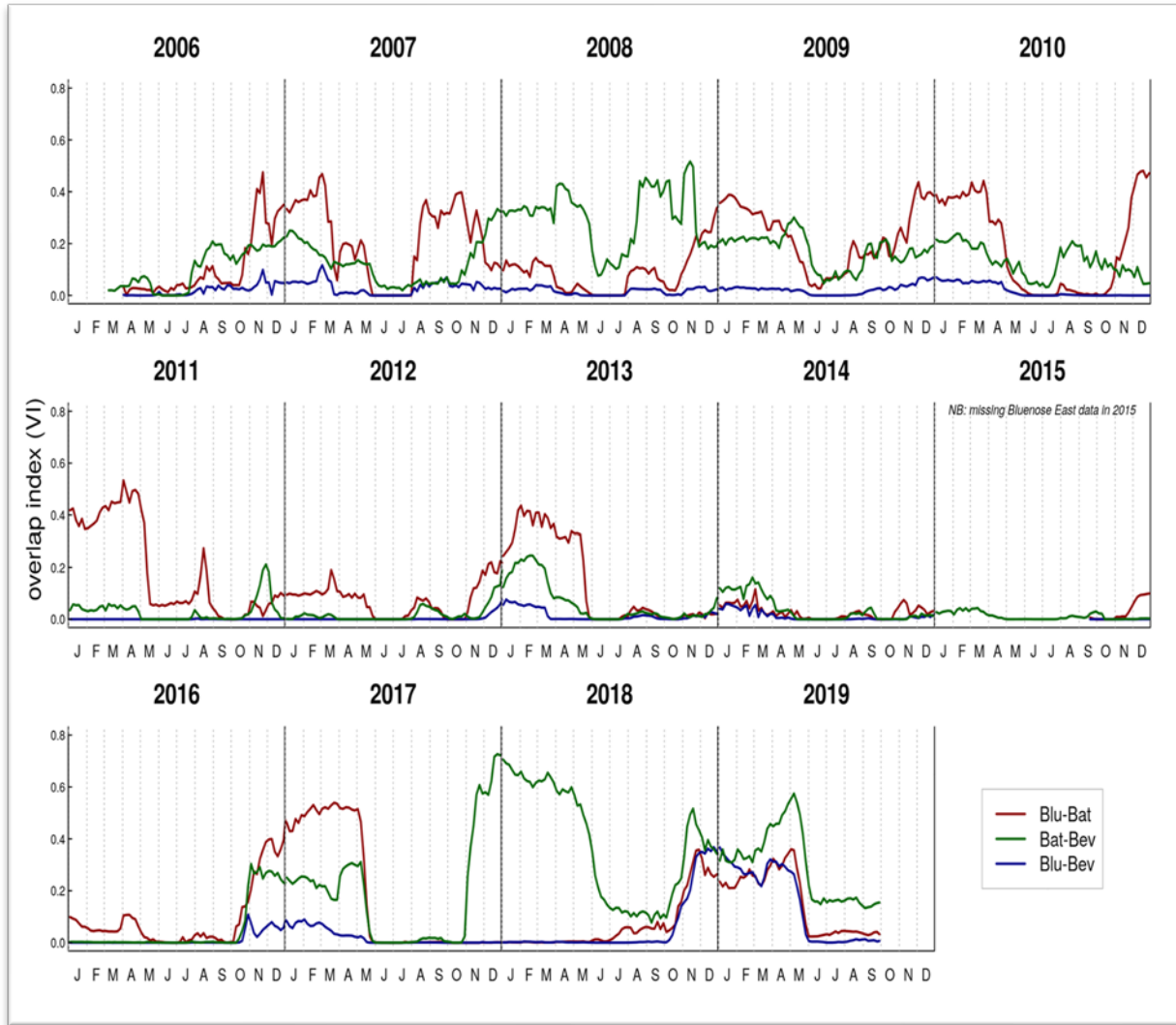
Figure 5. Estimated mean VI overlap by 5-day period throughout the year for all years since 2006 for each of the three pairs: Bluenose East and Bathurst (Blu-Bat, red lines), Bathurst and Beverly/Ahiak (green lines) and Bluenose East and Beverly/Ahiak (blue lines).

The aggregated results (Figure 6) also point to a two-stage increase in overlap post calving, to a generally low level in August through mid-October, and then a ramp up to relatively high levels in November through February (justifying our selection of November through February as a "winter" for the analyses in previous sections).
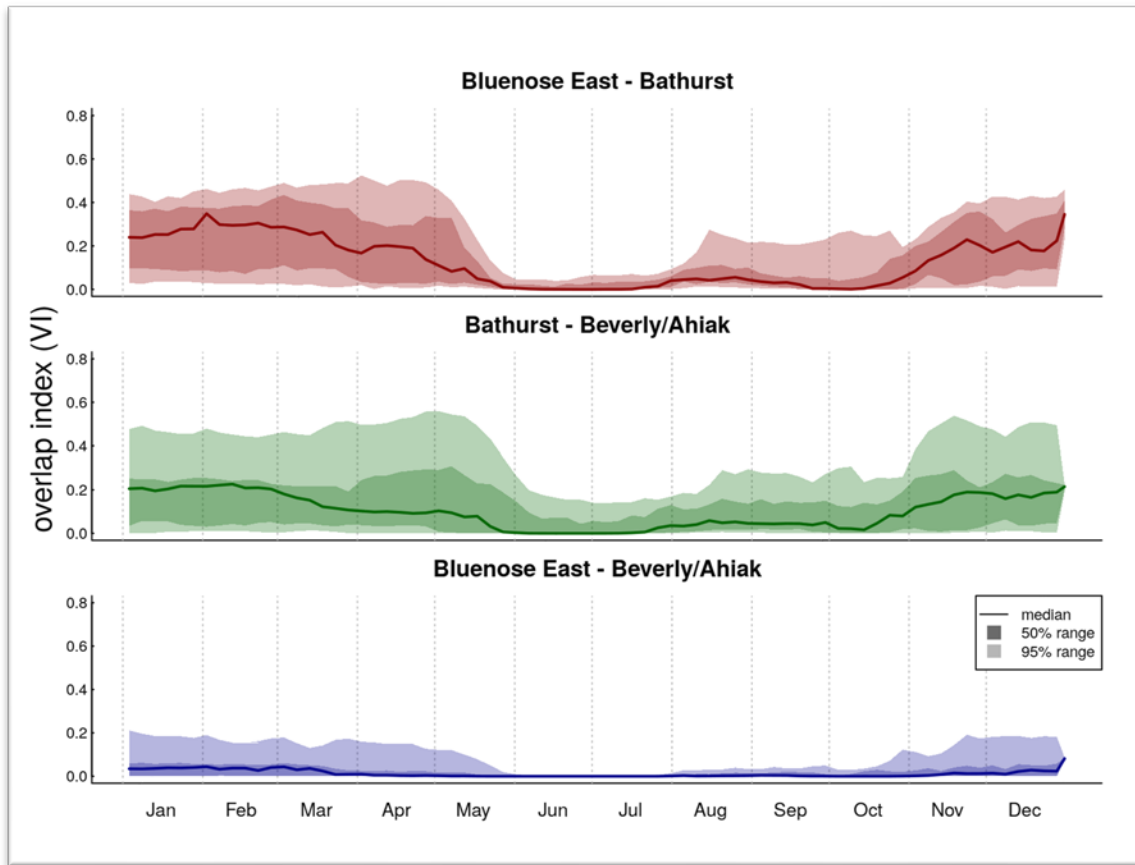
Figure 6. Median, inter-quartile range (darker shading), and 95% range (lighter shading) of herd-level VI overlap estimates by 5-day period 2005-2019.

In the winters of high overlap, there was a characteristic winter overlap profile (e.g. 2006-07, 2009-10, 2012-13, 2016-17) with Bluenose East-Bathurst [Blu-Bat] showing the highest levels of overlap (VI approx. 0.4) and Bathurst-Beverly/Ahiak [Bat-Bev] somewhat less (around 0.2). In other winters, (2011-12, 2013-14, 2014-15 - but there are few data from Bluenose East in most of 2014-15), winter overlap was much weaker (mainly below 0.1), and mainly for Blu-Bat. The two most recent winters show a switch as 2017-18 Bat-Bev had a high overlap (peaking at VI = 0.72 on December 24, 2017 - the highest values across all-time series) with zero Blu-Bat overlap. In 2018-19 all three herds showed a similar, relatively high level of overlap around 0.4, which were the highest values recorded for Blu-Bev, higher than Blu-Bat. In that 2018-2019 winter, all three herds essentially shared their winter range (as also seen in Figures 4 and 5).

In high overlap winters, the precise timing of the breakdown in overlap - corresponding to the separation of the herds for the pre-calving migration - is sharp and consistent (Figure 7). For example, Blu-Bat overlap plummeted from over 0.40 to under 0.01 between May 12 and May 24 in 2017, and from just under 0.4 to 0.01 between May 14 and May 28 in 2013. These dates correspond to the rather sudden beginning of the pre-calving migration to the calving grounds. The ramp-up in overlap in the preceding fall was more gradual and more annually varied, but the start is generally identifiable from the figures. In 2016, the increase began on Oct 4 (VI = 0.003), and reached values over 0.3 by November 18, whereas in 2012, VI was essentially throughout

October, but started increasing on November 3. In fall 2017, the notably high Bat-Bev overlap rapidly rose from 0.02 on October 30 to 0.57 by November 14, suggesting that the two herd's distribution merged quickly and stayed persistently overlapped throughout that winter.
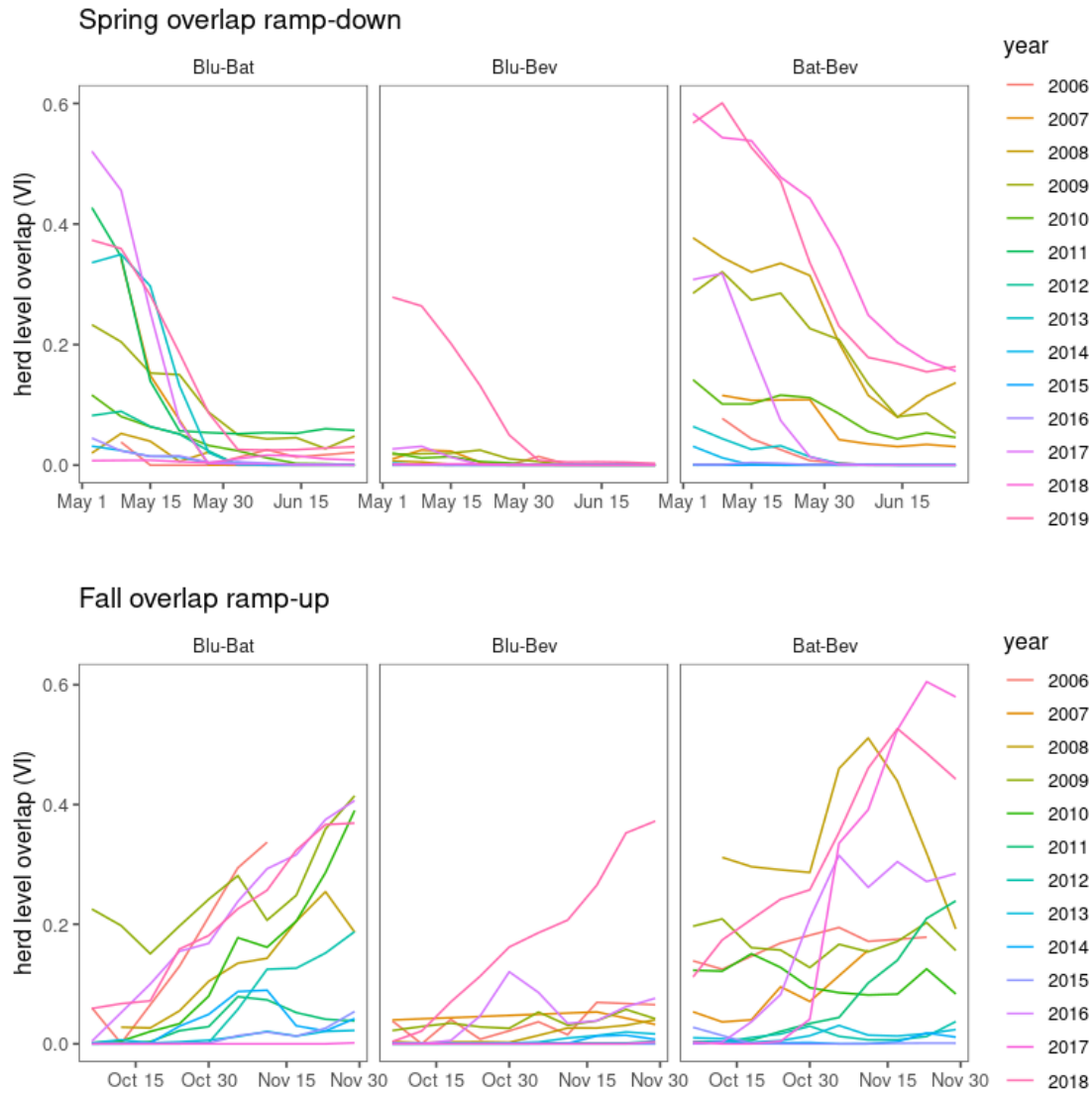
Figure 7. Annual comparison for the herd overlap showing the spring 'ramp-down' and fall 'ramp-up' for the Bathurst herd with the Bluenose East and Beverly/Ahiak herds.

3. Inter-individual distances

The proximity analysis looks in detail at inter-individual distances. Simply, we count the number of individuals within a set of distance thresholds (200, 100 and 50 m) on a given day. Although the majority of days have 0 encounters (even with 200 m, only 2314 days out of 7633 - 30%), there were marked peaks and patterns: notably, a distinctive peak in the immediate post-calving period, likely a reflection of insect harassment avoidance aggregations. Peaks, especially for the Bathurst

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in September / October, correspond to the fall migration and the rut. During most of winter there are nearly no close encounters among collared animals. Using the absolute number of such proximities for each of the three herds since 2015 reveals variation among herds: with Bathurst having the highest absolute values and Beverly/Ahiak the lowest (mean: 1.17, 3.98 and 0.44 for Bluenose East, Bathurst and Beverly/Ahiak, respectively). However, these values are highly dependent on the number of individuals collared, and on the overall area that is covered by those individuals. We note that the herds varied ten-fold in numbers of caribou.

For that reason, we developed a "corrected" version of the encounter metric, which takes the ratio of the observed number of encounters to the expected number of encounters given the available sample sizes and areas. Specifically, given an encounter radius r for n animals in an area A, the expected number of encounters is given by:

$$E(N_{enc.}) = \frac{\pi r^2 \, n(n-1)}{2A}$$

To obtain A (the overall area covered by the individuals), we compute a 50% kernel density around the individuals at each day, such that the area is a dynamic variable, as is the number of individuals with location data. The corrected encounter index is just the ratio of the observations to the expectation, divided by 1000: $I = N_{enc.obs}/E\,(N_{enc.})/1000$. We divide by 1000 because the observed number of encounters tends to be many orders of magnitude higher than any given expectation, reflecting both the intrinsic sociality of the animals and, likely, the much smaller practically available area (constraints of habitat suitability) than is captured by the utilization density, such that the values of the corrected index are, typically, between 0 and 10 rather than 0 and 10,000.

This index sharply alters the relative height of the encounter peaks (Table 4, Figure 8) especially the high mid-summer insect aggregations in 2018 and 2019 for the Bathurst herd. Also, accounting for the sample sizes and range area led to an otherwise obscured peak of encounters in the early spring pre-migration. The corrected encounter index was, overall, higher for Bathurst (mean 0.387, sd 1.86) followed by Beverly/Ahiak (0.10, sd 0.31) and Bluenose East (0.076, sd 0.16). The higher standard deviations reflect the highly skewed distributions, for which the median and even the 75% quartile for Beverly/Ahiak and Bluenose East are 0).
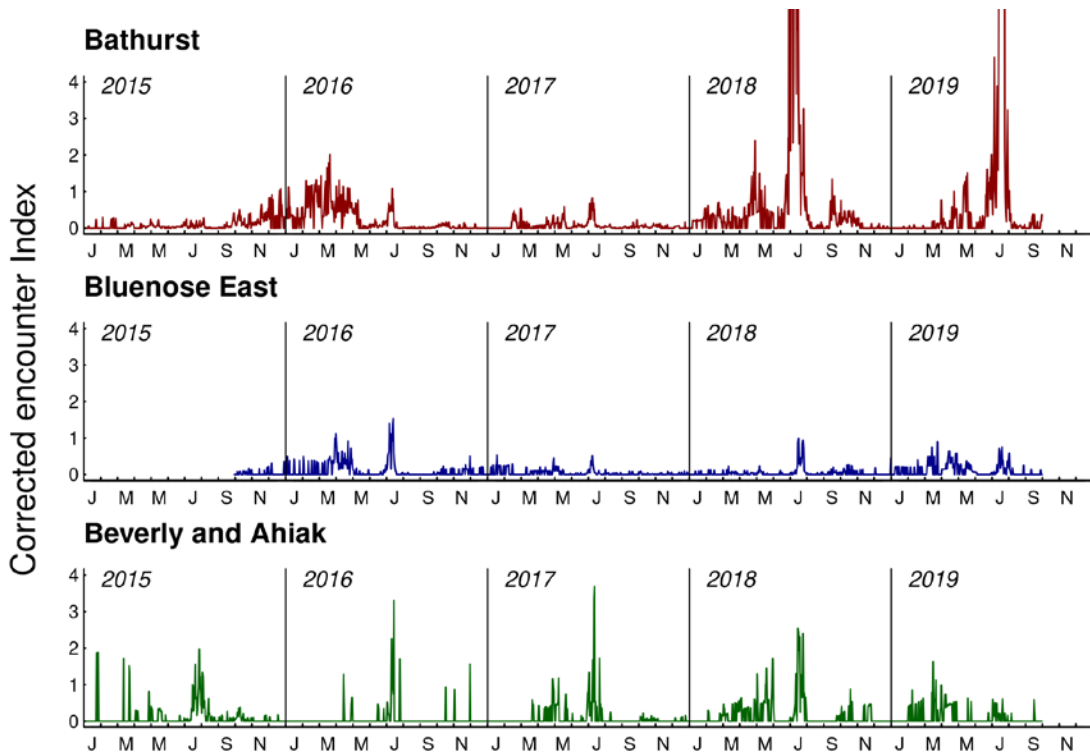
Figure 8. Corrected encounter index, showing the relative number of encounters relative to a null of uniformly randomly present individuals within an area the size of the 50% kernel of the animal locations on a given day (note y-axes differ in scale).

Table 4. The average number of daily encounters by year and month

Month	Bluenose East - Bathurst				Bathurst – Beverly/Ahiak			
	2016	2017	2018	2019	2016	2017	2018	2019
January	0	0.23	0	0.19	0	0.03	0.26	0.03
February	0	0.25	0	0.11	0	0	0.29	0.29
March	0	0.97	0	0.23	0	0.06	0.84	0.48
April	0.03	1.70	0	0.90	0	0.73	0.57	1.63
May	0	0.34	0	0.87	0	0.42	0.16	0.48
June	0	0	0	0	0	0	0	0
July	0	0	0	0.19	0	0	0.87	0.52
August	0	0	0	0	0	0	0	0.13
September	0	0	0	0.03	0	0	0.10	0.03
October	0.29	0	0.03	-	0	0	0.32	-
November	0.43	0	0.03	-	0	0.17	0.13	-
December	0.06	0	0.16	-	0	0.58	0.10	-

Table 5. The total number of unique 200 m encounters per day in the respective winters (October – May period). The numbers in parentheses reflect the mean number of collared individuals in each of those seasons.

Herd pair	2016-17	2017-18	2018-19	total
Bluenose East	117 (41.8)	105 (38.3)	162 (44.5)	384
Bathurst	209 (35.8)	391 (33.1)	336 (30.2)	936
Beverly/Ahiak	34 (25.1)	109 (38.8)	68 (33.5)	211
Blu-Bat	129	0	77	206
Bat-Bev	36	87	105	228
Blu-Bev	0	0	25	25

Lastly, we computed the total number of encounters *across* herds (Table 5) for three winters (October to May) where those encounters were available (2016-2019; Figure 9). Across those years, there were 459 such encounters (206 Blu-Bat, 228 Bat-Bev, 25 Blu-Bev). In 2016 and 2017, all of those encounters were Blu-Bat encounters. There were higher numbers of intra-herd than inter-herd encounters, though in 2018-19 there were only 68 encounters within Beverly/Ahiak, but 105 between Bathurst and Beverly/Ahiak animals, despite similar numbers of collared individuals (30.2 and 33.5, on average, throughout the winter). The time period of maximum cross-herd encounters was in the late winter / early spring before the spring migration began (mid-March to beginning of May), with very few encounters in the earlier winter months.
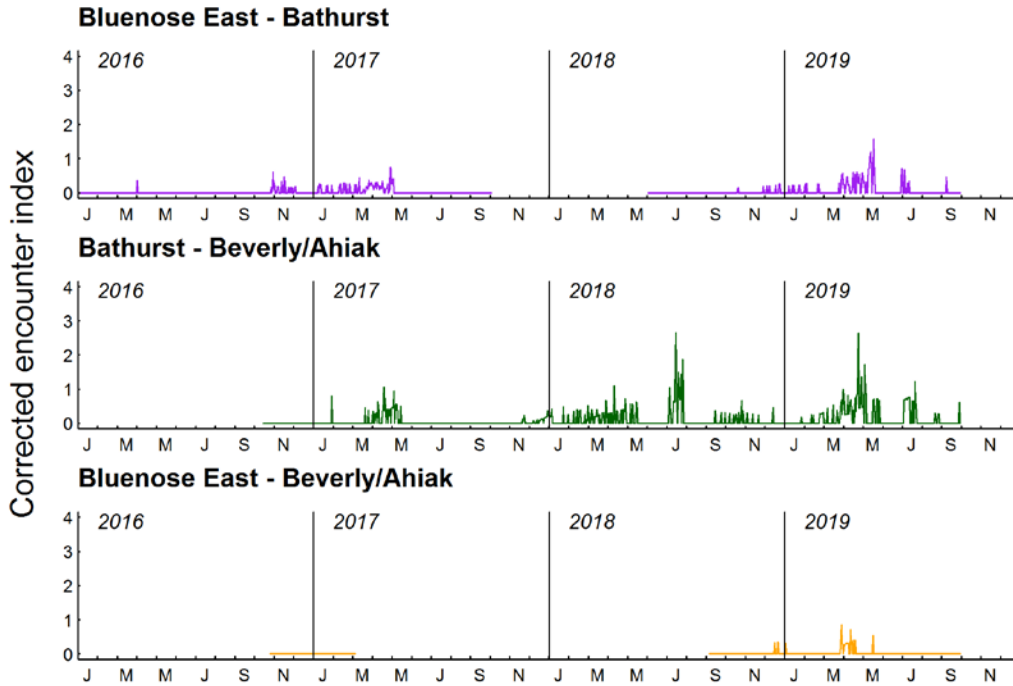
Figure 9. Numbers of encounters within 200 m of individual collared caribou across herds, color-coded as per the legend

We fit a generalized additive model (GAM) smooth to the corrected encounter index across day of year for each herd pooling all years, using a wrapped spline basis matching December 31 to January 1 using the gam function in the mgcv R package (Wood 2017). This analysis (Figure 10) reveals extremely consistent peaks in inter-individual encounters across all herds. Specifically, there is a marked peak in the middle of April, likely corresponding to staging prior to the initiation of pre-calving migration. A second peak near the beginning of July corresponding to insect harassment season, and a third peak in mid-October corresponding to the rut and fall migration. The markedly higher Bathurst peak likely reflects the declining herd size especially in 2018 and 2019. In general - as noted above - Bathurst herd, at extremely low numbers, tend to have higher aggregation indices than Bluenose East and Beverly animals.

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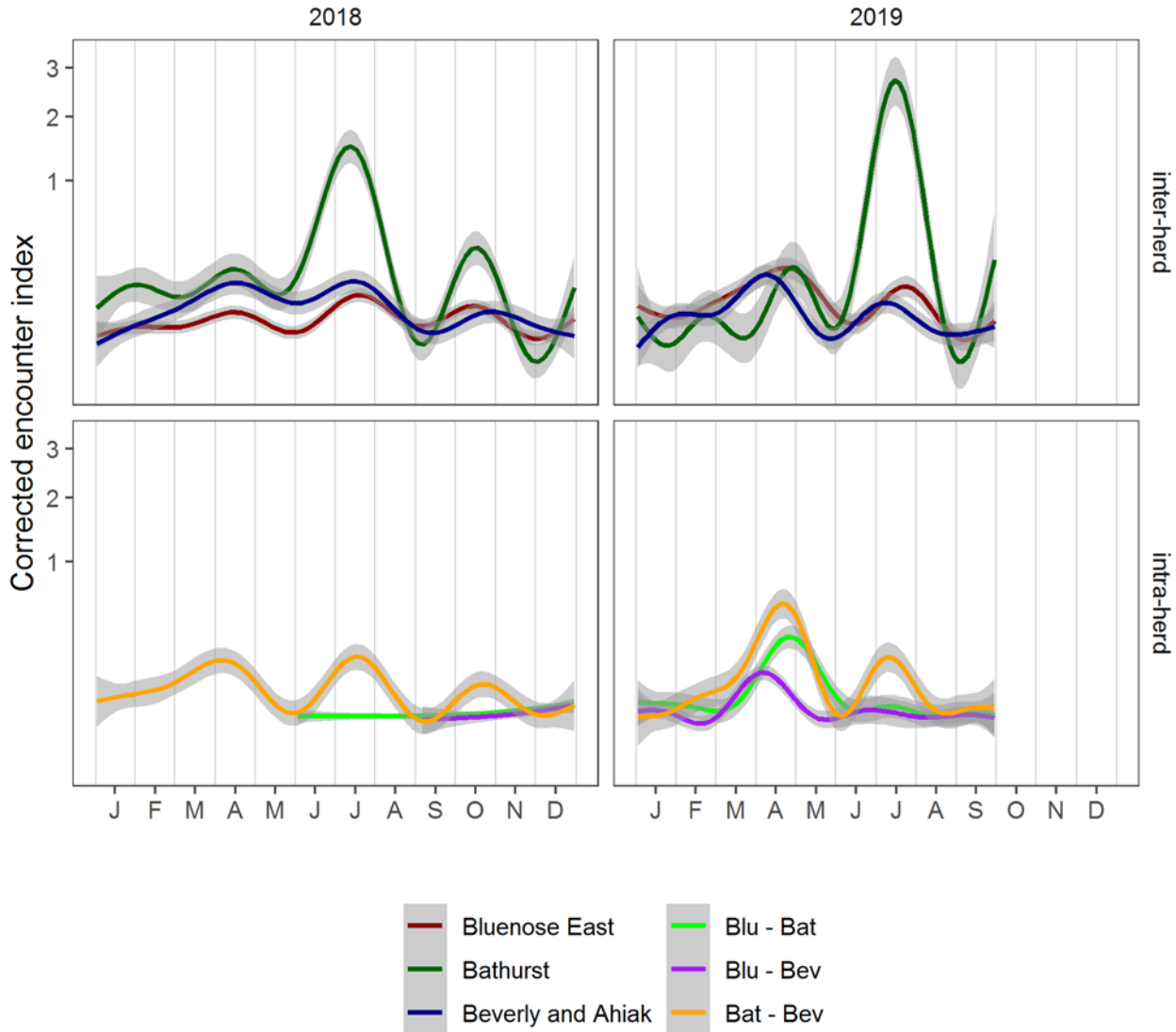
Figure 10. Corrected 200 m encounter index within herds by day of year. The curve represents a Generalized Additive Model smooth wrapped around the beginning and end of the year, the shaded area is in 95% confidence interval. Note, the data are presented on a square-root transformation

Discussion

At the herd scale, the Bathurst and its two neighboring herds annually varied in the extent of their winter overlap. Generally, over our study period (2005-2019), overlap between the winter distribution of the Bathurst and Beverly/Ahiak increased, especially in the most recent years. The overlap between neighboring herds begins early in winter (October) which is a previously undescribed finding. At the individual collared caribou scale, the timing of an increase in pairwise distances reveal that fall migration and rut can be discerned with a more defined peak. While annually variable (8-22 October), for the period 2014-2019, there is no trend in peak fall migration and rut compared to trend in the summer peak, which appears to be coming later in

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July. This leads us to acknowledge our results are preliminary as more detailed analyses could include the role of environmental variation such as summer droughts, fall plant phenology, snow conditions, and indices of insect harassment.

However, our current approach enabled us to meet our study objectives to measure the annual extent of winter range overlap between Bathurst, Bluenose East and Beverly/Ahiak herds. We report trends in annual overlap and the annual chronology of when the overlap develops at the herd scale. Our emphasis has been on applying indices such as the *Volume of Intersection Statistic* (VI) which meets Fieberg and Kochanny's (2005) recommendation for indices which are consistent with one's intuition of overlap and relatively easy to interpret. Our use of 'overlap' is somewhat similar to how Pritchard et al. (2020) defined overlap as the proportion of other herds predicted to be in the main range (defined as the 75% isopleth) of a herd. Both uses of overlap depend on kernel densities estimated from collared caribou. Pritchard et al. (2020) found a similar pattern of more overlap between neighboring herds in winter but aggregated their results for 2003-2015 rather than examine inter-annual variation.

At a finer scale, the individual collared cow, we examined within and between herd spacing relative to each other as a measure of encounters. As we organized the database and developed the analyses, we noted that in the database the limitation from low sample sizes (number of collared individuals) has been slowly resolving over time. Collaring began in 1996, but we used the period 2005-2019 when sample sizes were adequate. Our selection of timescales of annual or 6 days minimizes any problems arising from types of collars (satellite or GPS), different duty cycles of the collars, while our – at minimum – every other day sub-sampling resolves issues of autocorrelation. Although males (prime and older males) can be relatively segregated from females, especially later in winter and pre-calving migration, the number of collared males is low compared to the females and would not alter the overall distribution patterns.

We also did not separate out non-breeding cows, whose migration to the calving ground is slower, and we also did not screen out the few Bathurst collared cows in 2018 and 2019 which emigrated to the Beverly/Ahiak calving grounds (Adamczewski et al. 2019a, b). This emigration and a shift in calving distribution (Figure 11) are reflected in a higher overlap index for Bathurst and Beverly/Ahiak (Figure 8). The emigration may either been a consequence of overlapping winter distribution (Adamczewski et al. 2019a) or the response to the continued decline and consequent low densities of cows on the Bathurst calving grounds (Gunn et al. 2012, Adamczewski et al. 2015). The overlap between Bluenose East and Bathurst herd winter ranges did not result in emigration to either herd's calving grounds (Boulanger et al. 2019).
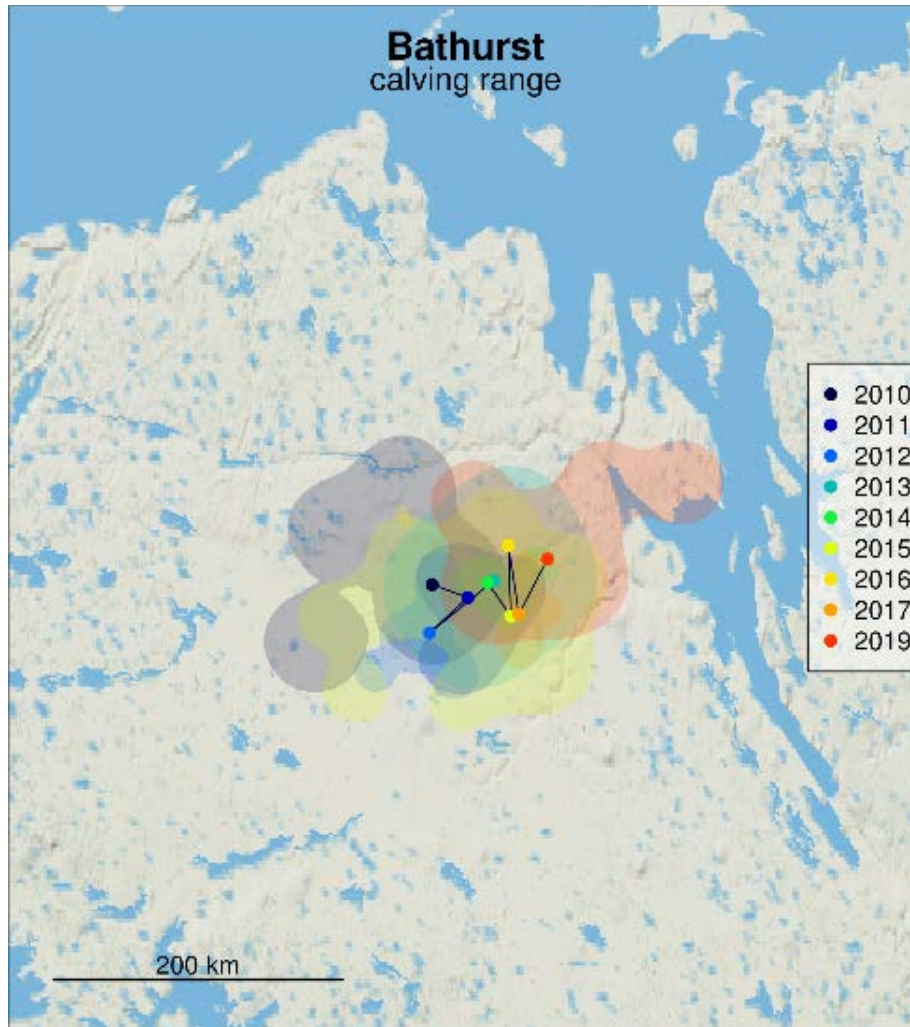
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Figure 11. Annual overlapping polygons (95% kernel) and centroids for the Bathurst herd calving range (Couriot et al. In prep. unpublished analysis of parturition locations).

The outstanding behavioral characteristic of migratory tundra caribou is that they are gregarious, but investigations into how that collective behavior underlies distribution and migratory patterns are markedly few (Dalziel et al. 2015, Torney et al. 2018). Additionally, Fryxell et al. (2009) commented on the lack of a theoretical framework to link functional relationships between physiological state, prior experience, and landscape characteristics. Our indices at two scales (herd and individual encounters) while not designed to investigate collective behavior relative to environmental variation did reveal complexity and differences relative to the two scales. Interestingly, we did find a relationship with herd size and trends. The changing relationship between the Bathurst herd with its two neighboring herds occurs as the Bathurst herd has continued to shift its winter ranges. The Bathurst herd's winter range has shifted northeast since 2016 (Figure 12) which coincides with overlap with the Beverly/Ahiak herd.
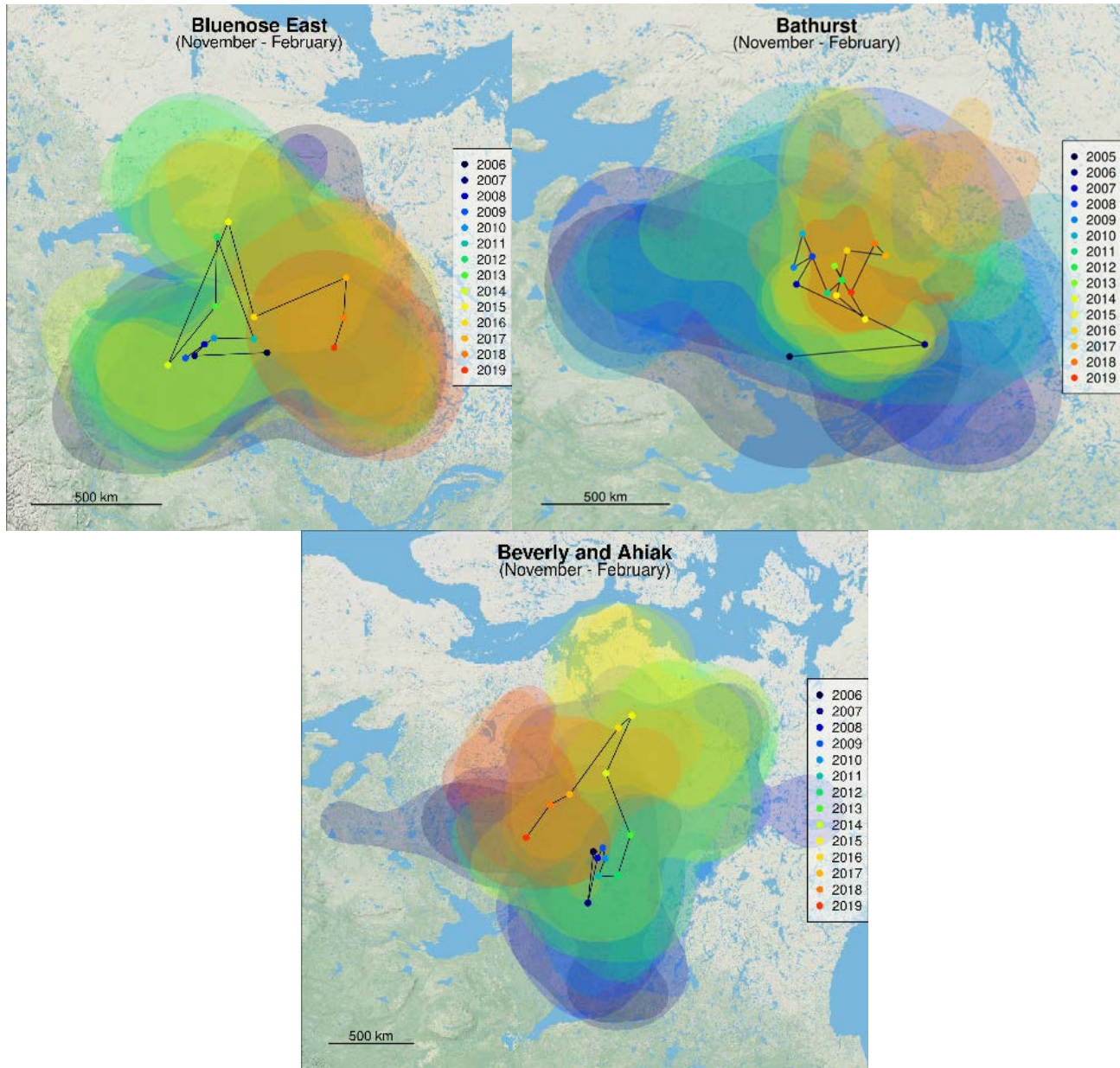
Figure 12. Annual overlapping polygons (95% kernel) and centroids for Bluenose East, Bathurst and Beverly and Ahiak herd winter range.

The relationship between shifts in the Bathurst herd's winter ranges and neighboring herd winter ranges differs from what Le Corre et al. (2019) reported for the George River herd of migratory tundra caribou in northern Quebec. The George River herd also shifted its winter range during the herd's decline but the shift reduced overlap with winter range of the neighboring Leaf River herd. Our analysis suggests overlap is more likely as herds decline sharply in abundance and winter ranges shift. But we do not have collar data for the period when herds were at their peak abundance and Bathurst winter ranges were larger and located either west or south of Great Slave Lake (Gunn et al. 2013).

The individual collared caribou encounters corrected for range size revealed that a peak for fall migration was detectable although it was lower than for pre-calving migration and both were lower than aggregations in July (Figure 7). Less attention has been paid to fall compared to pre-calving migration. An exception is Le Corre et al (2017) who examined the timing of departure after the rut and arrival to the winter range for the George River and Leaf River herds. Arrival date on the winter range was earlier when herds had declined and reduced migration distances also had earlier arrivals. Snow conditions during the migration also affected arrival time on the winter range (Le Corre et al. 2017). Our approach to measuring the herd overlap and the encounter rates for individual collared caribou was not designed to investigate how environmental variation and collective behavior shape the migratory pathways (Figure 13).

Figure 13. Fall migration for the Bathurst herd crossing a newly frozen lake, October 2004.

The interesting point about the cross-herd encounters was their relatively low number even although the extent of overlap at the herd scale was high in some years. The maximum number of encounters were in late winter before the pre-calving migration (mid-March to beginning of May), with very few encounters in the earlier winter months. This peak likely reflects the increase in group sizes as caribou start to stage prior to pre-calving migration (unpubl. observations and see cover photograph). The importance of group sizes during migration is increased sharing of information and experience as well as likely energetic efficiencies (Torney et al. 2018, Berdahl et al. 2016). Although the encounters between collared caribou from the Bluenose East and Bathurst herd was high in May 2017 and 2019, it did not result in calving ground switches (Boulanger et al. 2019). However, switches of 3 of the 11 collared Bathurst herd cows to the Beverly/Ahiak's herd

calving ground in 2018 and 2019 (Adamczewski et al. 2019b), did coincide with the higher rate of cross-herd encounters in May 2019. Both the Bathurst and Beverly/Ahiak migrate northeast from their winter to calving ranges and previously (2001 and 2002), collared cows shred initial pre-calving migratory pathways (Gunn and D'Hont 2002).

Annually, tracking the extent and timing of overlap between neighboring herds is an essential contribution to assigning harvests and predation rates which are managed at the herd scale. Additionally, monitoring overlap and its timing can identify 'surprises' in the sense of unexpected changes and which may have implications for other monitoring such as vital rates and herd size. For those applications, the Volume Index and Encounter rate meet criteria to act as indicators (Tyler 2008) for which we can establish benchmarks and thus contribute to the adaptive co-management framework for the Bluenose East and Bathurst herds. Lastly, we suggest that the indicators are a relatively simple and robust approach to investigating the relationship between wolves (if collared) and caribou at the herd and individual scale.

Acknowledgements

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Appendix A. Assessment of bias

We checked whether a significant bias is introduced by using daily mean locations versus subsampled locations when estimating VI indices. It is expected that highly auto-correlated data will lead to density kernels that are too small (i.e. too tight around the track rather than capturing an entire range). For that reason, we estimated the herd-level overlap for the full data (i.e. daily mean locations) versus a thinned sample (every 5 days). There is a consistent underestimation of the overlap for the full data, but the absolute values of the estimated overlap are quite similar (Figure A.a). The bias, however, is most notable at small values of overlap (Figure A.b). Specifically, the bias is 40% at low overlap (VI ≤ 0.1), 8% at intermediate overlaps (0.1 ≤ VI ≤ 0.5), and 3% at high overlaps (VI > 0.5). Based on these results, we prefer to use thinned data for overlap analysis. For individual overlaps, however, to increase the sample size, we only thin the data to every second day.

Figure A. Overlap estimates using thinned data (x-axis, both panels), overlap from the full data (y-axis in a) and approximate bias (ratio in y-axis b). The grey line in (a) is equality, the shaded region in (b) is a loess smooth with confidence intervals,
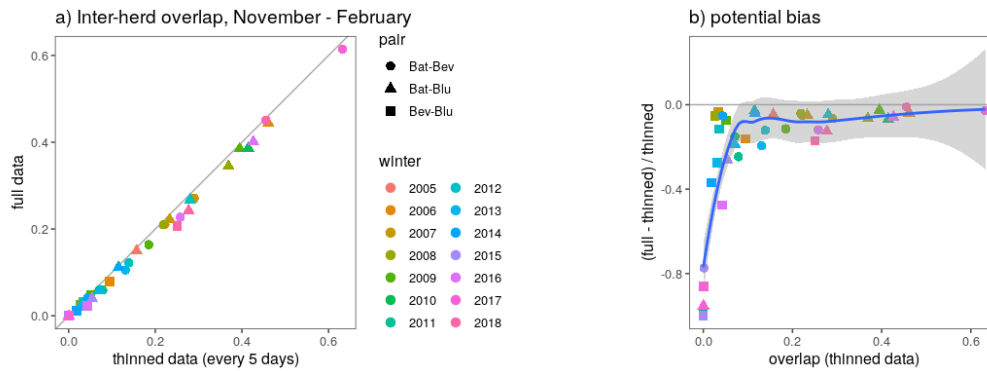
Appendix B. Movebank data repository for Bluenose East, Bathurst and Beverly/Ahiak herds

The caribou locations in the Movebank repository are from caribou collared on their winter ranges which may overlap between neighboring herds. GNWT wildlife biologists and Movebank staff (B. Fournier, A. Kelly and S. Davidson) manually associated individual caribou in the dataset based on calving location to one of 8 so-called "habitat" categories which correspond, roughly, to the herds. The corresponding raw numbers of observations for these animals are in table 2, and the distribution of these habitats across the Movebank studies is illustated in Figure 1.

Table 1: Summary of herd and dates for caribou data held in Movebank Repository.

Movebank repository	No. individuals	No. locations	Start	End
Bluenose East	210	190195	2005	2019
Bathurst	362	532646	1996	2019
Beverly / Ahiak	175	245791	1995	2019
total	747	968632	1995	2019

Table 2: Summary of telemetry data sets by "habitat" attribution.

Habitat	No. individuals	No. obsevations	Start	End	Longitude
Bluenose East	258	285143	2005	2019	116.6
Bathurst	201	315852	1996	2019	111.1
Beverly	149	277379	1995	2019	106.4
Beverly and Ahiak	33	39110	2012	2017	103.4
Ahiak	7	10591	2006	2014	100.9
Qamanirjuaq	3	5819	2006	2016	99.9
unknown	96	34738	1996	2019	110.3

To clarify the herd assignments in the raw data, we performed a cluster analysis on all the caribou by calving location and separated the animals into three herds of interest (Bluenose East, Bathurst and Beverly/Ahiak). This classification excluded 3 animals that were classified in the raw data as "Qamanirjuaq" (as intended) and assigned a calving ground and herd to the Unknown animals. Details of the classification are in the **Appendix** [*or supplemental file prepared by Ophélie*].

The resulting dataset contains 619 individuals (176 F and 70 M from Bluenose East, 153 F / 37 M for Bathurst, and 151 F / 32 M for Beverly/Ahiak), with average durations about 576 days of observation (inter-quartile range: 276-938).

Appendix C. Individual and herd winter overlap across years 2006 - 2007
(file available separately)