Annual variation in the seasonal range overlap between the Bathurst, Bluenose East, and Beverly caribou herds

Contract report for

Wek’èezhìı Renewable Resources Board

by

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Executive Summary

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

To increase understanding of the overlapping winter ranges, the WRRB initiated analyses of caribou distribution using the Government of the Northwest Territories collared caribou. We 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. We applied an index to measure the overlap and found that, since 2005, the overlap between the winter distribution of the Bathurst and Beverly herds increased, especially in recent years. The presence and extent of the overlap between the neighboring herds varied during the 16 winters we examined. The overlap between the Bathurst herd and at least one of its neighbors was minimal for only 3 - 5 years of the 16 years we examined. The Bathurst herd has recently shifted its winter distribution northeast which reduced overlap with the Bluenose East herd and increased overlap with the Beverly herd. Additionally, the Beverly herd shifted its winter distribution north and west.

The overlap starts relatively abruptly in early winter (October) and persists through the winter until ending in May at the beginning of pre-calving migration. The overlap between individual collared caribou either within a herd or across herds at the herd scale is less measurable at 200m resolution . The individual encounter rate was highest for the Bathurst herd, the smallest of the three herds. In other words, collared caribou in the Bathurst herd were more like to encounter one another than were collared caribou in the Beverly or Bluenose East herds.

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1 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, Rettie, and Coulton 2017). In recent years, shifts in the winter ranges for the Bluenose East, Bathurst, and Beverly herds have led to overlapping winter distribution between the herds which has complicated monitoring and assigning harvest allowances. 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 on winter distribution contributed to the the WRRB's uncertainty about the reliability of harvest information (Wek'èezhìı Renewable Resources Board 2019b).

The Government of the Northwest Territories (GNWT) suggested that winter overlap between neighboring herds may affect the likelihood of cow caribou switching calving grounds, as happened in 2018 and 2019 (Adamczewski et al. 2019a; Wek'èezhìı Renewable Resources Board 2019a). However, GNWT did not analyze trends in winter distribution, the extent of overlap, or how it may affect pre-calving migration. In addition to being concerned about assigning harvest quotas when neighboring herds overlap their winter distribution, the WRRB is concerned about emigration. An apparent increase in the number of females from the Bathurst herd that migrate with Beverly or Bluenose East caribou to their calving grounds is thought to be a factor in the persistent decline of the herd. Subsequently, GNWT shared caribou collar data with the WRRB to undertake analyses of winter distribution and especially the overlap between neighboring herds.

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 since collar data can provide valuable insight. Ensuring that collar information is used to the best extent possible and contributes to caribou management helps to justify collaring.

The goal of this preliminary analysis was to measure the annual extent of seasonal range overlap between Bathurst, Bluenose East, and Beverly herds. We describe trends in annual overlap and chronology of when the winter overlap develops at the herd scale. At a finer scale, the individual collared caribou, we examined within- and between-herd spacing relative to other collared caribou 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.

2. Methods

2.1 The caribou herds

During our study period (2006-2021), the Bluenose East, Bathurst, and Beverly herds were declining (Wek'èezhìı Renewable Resources Board 2019a). The Bathurst herd declined from a 1986 peak of 470,000 to an estimate of 19,800 in 2015; the decline then accelerated to approximately 29% a year, dropping the population to 8,207 in 2018 (Wek'èezhìı Renewable Resources Board 2019a). The Bluenose East herd has declined 81% since the

2010 estimate of 103,000 relative to the 2018 estimate of 19,300 caribou (Wek’èezhìı Renewable Resources Board 2019b). Changes in calving distribution in the 2000s and differences in their interpretation have complicated describing declines in the Beverly herd (COSEWIC 2016). Campbell et al. (2019) report that the Beverly herd declined from 136,600 in 2011 to 106,000 estimated in 2018.

2.2 Data

Collared animal movement data collected primarily by GNWT-led monitoring efforts since 1998 were downloaded from the Movebank repository (http://movebank.org, accessed Sep 2022). The data are organized in “studies”: *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 more than 1 million locations collected from 852 individuals starting as early as spring 1995 and extending until winter 2021 (Table 1).

Table 1: *Number of caribou collared by year from the Movebank data repository.*

Year	Bluenose East	Bathurst	Beverly
1995	0	0	1
1996	5	8	1
1997	6	7	1
1998	5	18	0
1999	4	15	0
2000	4	15	0
2001	0	14	0
2002	0	10	0
2003	0	11	0
2004	0	13	0
2005	4	13	0
2006	14	13	14
2007	8	19	24
2008	26	26	42
2009	55	19	40
2010	52	23	25
2011	30	20	16
2012	67	24	27
2013	50	17	17
2014	37	20	32
2015	59	46	51
2016	55	46	38
2017	57	49	57
2018	51	42	62
2019	59	42	57
2020	73	69	34
2021	46	48	18

Due to variability in the herd assignments in the raw data, we performed a cluster analysis on the average daily June locations of caribou (i.e., the centroid of the locations of a given animal on a given day) and separated the animals into three herds of interest (Bluenose East, Bathurst, and Beverly). After removing animals that belonged to other herds or that remained unclassified and keeping years when annual collar sample size was >10 for all three herds (i.e., years after 2005), the resulting dataset contained 852 individuals (233 F and 88 M from Bluenose East (plus 5 unsexed), 227 F / 69 M for Bathurst (plus 1 unsexed), and 168 F / 61 M for Beverly) (Table 2). The duration of collar transmitting varied (Figure 1) and the average duration was about 573 days (inter-quartile range: 164-823).

Table 2: *Sample size (collar numbers) by year and by herd, assigned using a cluster analysis.*

Year	Bluenose East	Bathurst	Beverly
2006	14	19	16
2007	10	23	29
2008	27	32	45
2009	59	25	38
2010	51	26	25
2011	30	21	17
2012	64	26	25
2013	49	18	16
2014	35	20	30
2015	59	46	51
2016	52	47	38
2017	56	54	55
2018	51	48	60
2019	59	47	57
2020	74	66	35
2021	81	63	50

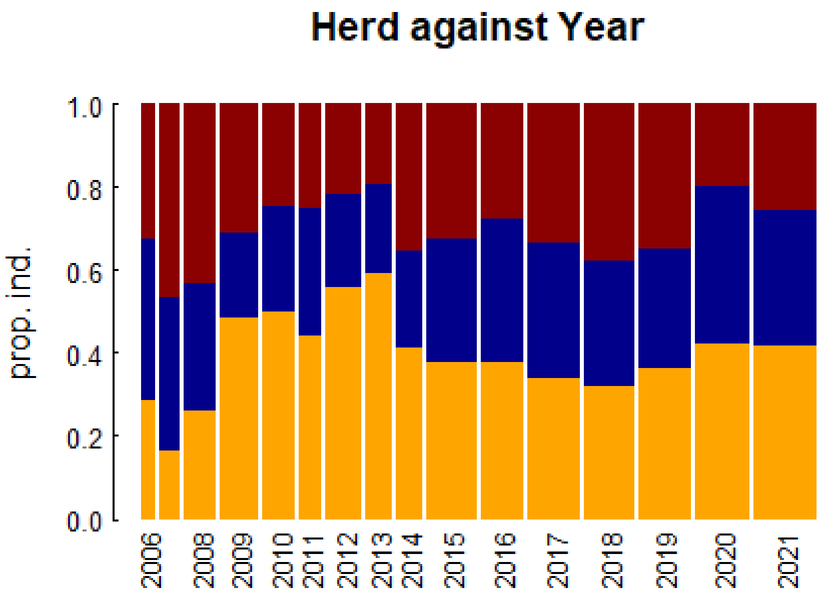

Figure 1. *Proportion of collared animals belonging to each of the three herds (Bluenose East – yellow; Bathurst - blue; Beverly – dark red). Widths of bars are proportional to the total number of collared individuals in a given year.*

2.3 Intra- and Inter-herd winter overlaps

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 accounting for differences in the relative probability of space-use throughout estimated utilization distributions (UD's). To that end, we selected the Volume of Intersection Statistic (VI) which is defined as $VI=\int min(UDi, UDj)dA$, where the UD is a probability distribution of finding an animal at a given point, estimated using bivariate normal kernels (Benhamou and Cornélis 2010).

The VI is an asymmetric index ranging from 0 to 1 that captures the shared volume of the overlap of kernel densities (e.g., 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.

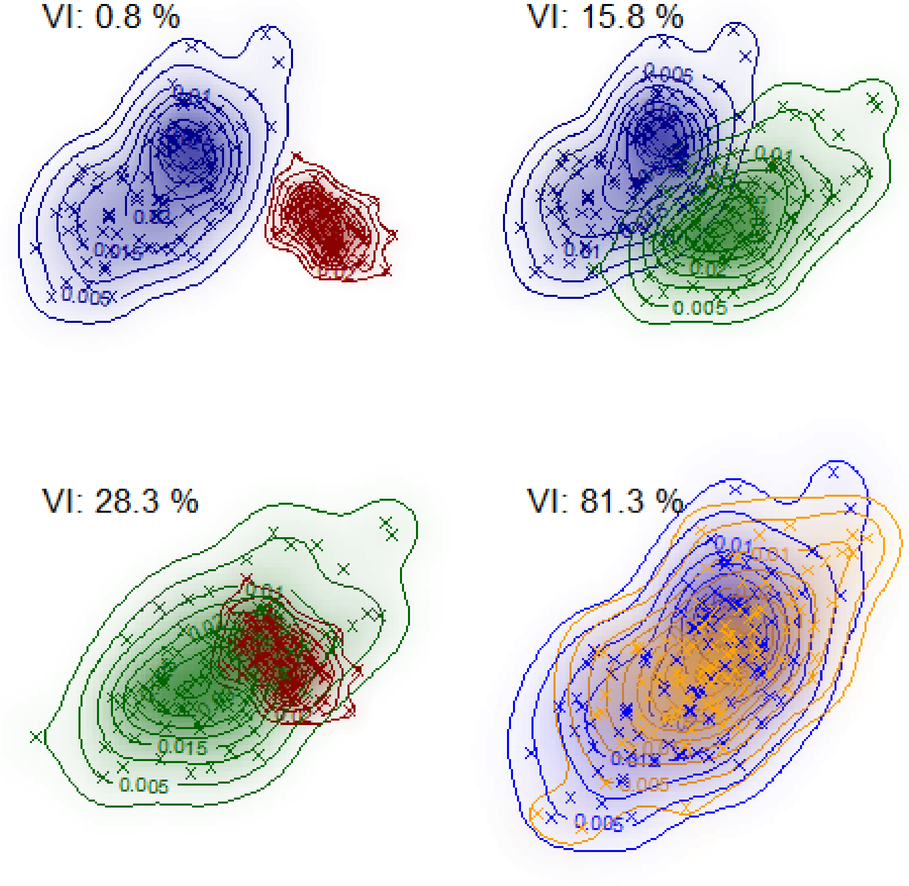

Figure 2. *Examples of various levels of volume intersection (VI) overlap index for four different pairs of simulated data. The "x"s represent 100 simulated locations for the blue, red, green and yellow populations and the shaded areas and contour lines represent the estimated utilization density. In the last (bottom right) example, with the highest overlap, the two samples were drawn from the same distribution.*

We computed VI indices for each year across herds and across individuals during winter, defined as November 1 - March 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 (data available on request).

2.4 Seasonal dynamics of inter-herd overlap

To look more closely at the seasonal dynamics of overlap, we also looked at inter-herd overlaps across the entire 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. We then computed VI overlaps among herds per period. This allowed us to explore more closely the variation of the overlap within and across herds through the entire year. We expected the overlap among herds to be low during the calving season and summer, and to increase during or after fall migration.

2.5 Inter-individual distances

We used a proximity analysis to describe a more detailed, alternative, look at inter-individual distances to estimate an encounter rate. We counted the number of collared individuals within a given set of distance thresholds (200, 100 and 50 m) of each other on a given day and used the pairwise distances between collared individuals as a metric of social interaction and grouping. In other words, the more times two collared individuals were within the distance thresholds of each other, the more aggregated the herd(s) were assumed to be. We examined pairwise distances within herds (intra-herd) and across herds (inter-herd).

Although the majority of days had 0 encounters (even with 200 m, only 2,314 days out of 7,633; 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 in September - October, correspond to the fall migration and the rut. During most of winter, there were 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 the lowest (mean: 1.17, 3.98 and 0.44 for Bluenose East, Bathurst, and Beverly, respectively). However, these values were highly dependent on the number of individuals collared, and on the overall area covered by those individuals. We note that the herds varied ten-fold in numbers of caribou. We therefore 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 computed a 50% kernel density around the individuals each day, such that the area is a dynamic variable, as is the number of individuals with location data. The corrected encounter index is the ratio of the observations to the expectation, divided by 1,000:

$$I = \frac{N_{enc.obs}}{E(N_{enc.})} * \frac{1}{1e3}$$

We divided by 1,000 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.

3 Results

3.1 Intra- and Inter-herd Overlaps

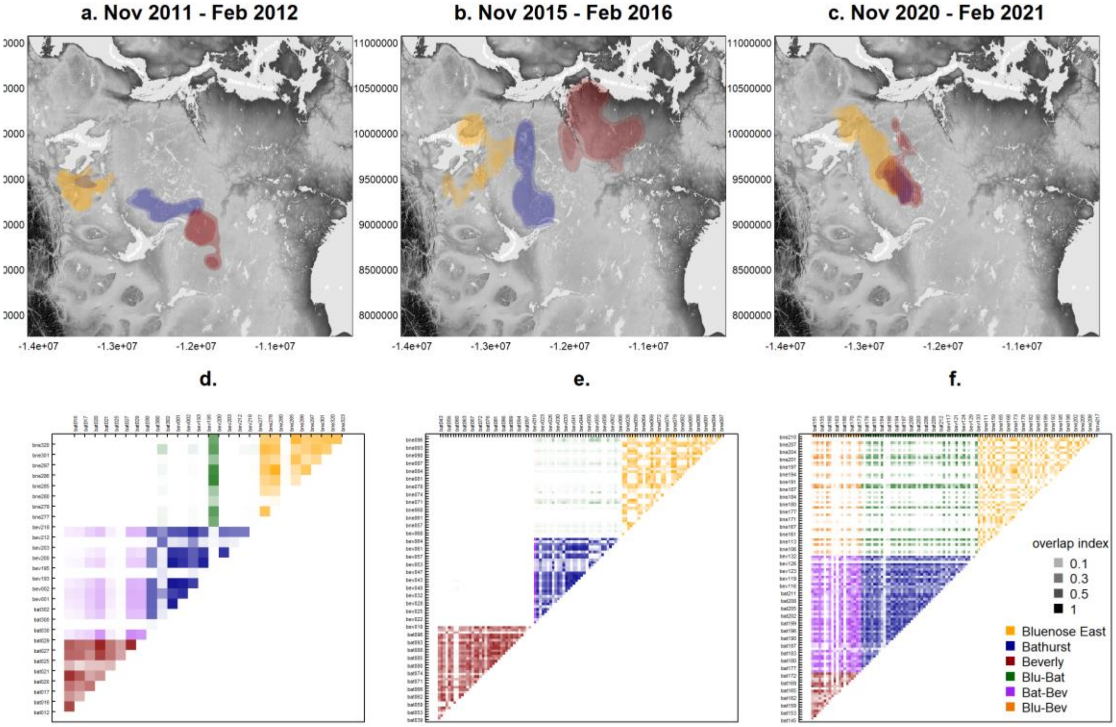

Figure 3. *Top panels - estimated winter (November 1 - Feb 28) utilization distributions (UD) in three well-contrasted years (left to right: 2011-12, 2015-16, 2020-21), Bluenose East, Bathurst and Beverly animals in yellow, blue and red, respectively. Lower panels - individual overlap matrices, where each square indicates a single overlap value across individuals. Within-herd overlaps are in yellow, blue and red, as above, while inter-herd overlaps are in off-diagonal blocks in mixed colors.*

As an initial step, we mapped the winter distributions as utilization distributions since 1997 for the Bathurst herd with the overlap with neighboring herds (available as a separate file on request). Using three well-contrasted winters (2011-12, 2015-16, 2020-21), we summarized the overlaps across herds as individual collared caribou overlap matrices (Figure 3). The variation in latitude (southernmost in 2011-12, northernmost in 2015-16) was noticeable and suggests a trend in the Bathurst and Beverly herds' winter distributions shifting north.

The median overall VI overlap was highest for Bluenose-East - Bathurst compared to the Bathurst - Beverly and Bluenose East – Beverly VI overlaps (Table 3). However, the VI overlap varied annually (e.g., in 2011-12, Bluenose East - Bathurst and Bathurst - Beverly overlapped 11.1% and 5.95%, respectively, compared to 21.14% and 70.28% in 2020-21 (Table 4, Figure 3)). A linear regression for the VI overlap between the Bathurst and its two neighboring herds revealed changes over the period 2006-2021 with the Bathurst - Bluenose East VI overlap slightly decreasing (decrease of 1.2% per year, p-value = 0.16, r^2=0.14) and Bathurst - Beverly VI overlap increasing (increase of 2.9% per year, p-value = 0.02, r^2=0.35).

***Table 3.* Median and 25% and 75% quartiles for overall VI overlap between pairs of neighboring herds, 2006-2021.**

Herd pair	Median	Q25	Q75	Min	Max
Bluenose East - Bathurst	23.81	11.30	31.95	3.35	47.46
Bathurst - Beverly	18.95	8.10	28.58	0.01	70.28
Bluenose East - Beverly	2.26	0.01	4.49	0.00	22.91

***Table 4.* Estimated mean VI overlap for the pairwise comparisons for the Bluenose East, Bathurst and Beverly herds, 2006-2021.**

Winter	Bluenose East - Bathurst	Bathurst - Beverly	Bluenose East - Beverly
2006-07	24.31	10.26	2.33
2007-08	25.38	30.17	0.00
2008-09	35.40	12.89	0.01
2009-10	47.46	18.95	5.79
2010-11	37.55	0.01	0.00
2011-12	11.10	5.95	0.00
2012-13	28.50	19.67	3.24
2013-14	5.70	10.52	2.26
2014-15	11.51	4.12	1.03
2015-16	4.17	3.29	0.09
2016-17	42.66	26.99	5.75
2017-18	3.35	62.34	0.02
2018-19	23.81	49.44	20.42
2019-20	15.10	24.65	3.21
2020-21	21.14	70.28	22.91

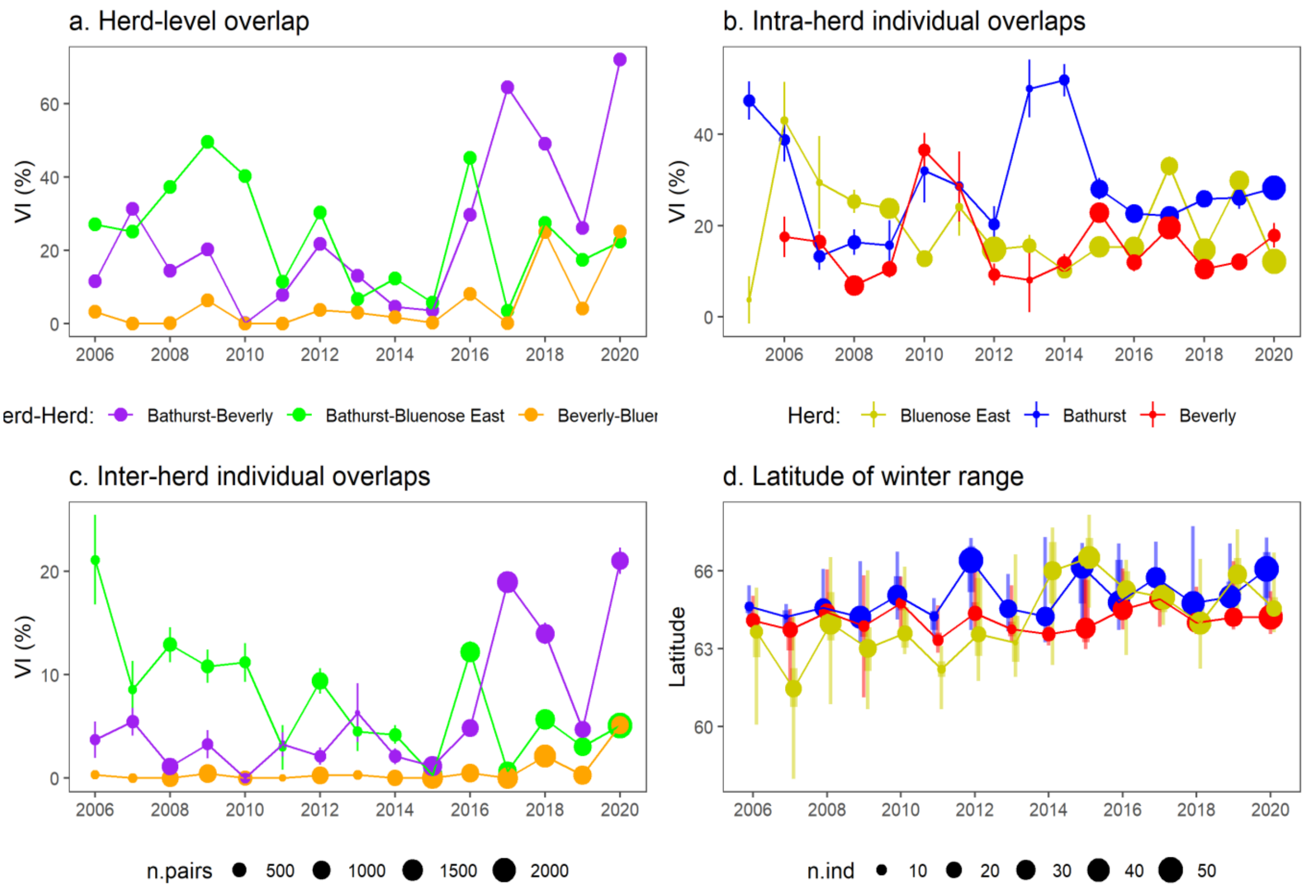

Figure 4. *Estimated VI overlap at (a) herd level, (b) among individuals within a herd and (c) among individuals across herds. Vertical bars in (b) and (c) indicate 95% standard error around the means, and size of circles represents number of pairs. Panel (d) shows the median (circle), inter-quartile 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 for intra- and inter-herd varied across years (Figure 4, Table 4). In the early years (e.g., from winter 2006-07 to winter 2012-13), there was a characteristic winter VI overlap profile, with Bluenose East - Bathurst (Blu-Bat) showing the highest levels of VI overlap (VI approx. 0.3) and Bathurst - Beverly (Bat-Bev) somewhat less (VI less then 0.2). In other winters, (2013-14 to 2015-16), winter VI overlap was much weaker (mainly below 0.1) among all pairs of herds. The most recent winters show a switch, as Bat-Bev had a high VI overlap (peaking at VI = 0.7 during winter 2020-21). In 2018-19 all three herds showed a similar, relatively high level of VI overlap (higher than 0.2), which was the highest value recorded for Blu-Bev. In that 2018-2019 winter, all three herds essentially shared their winter range (as seen in Figures 4 and 5).

3.2 Seasonal dynamics of herd overlap

As expected, the VI overlap among herds decreased during spring, to be close to zero during calving and summer, then increased during fall (figure 5).

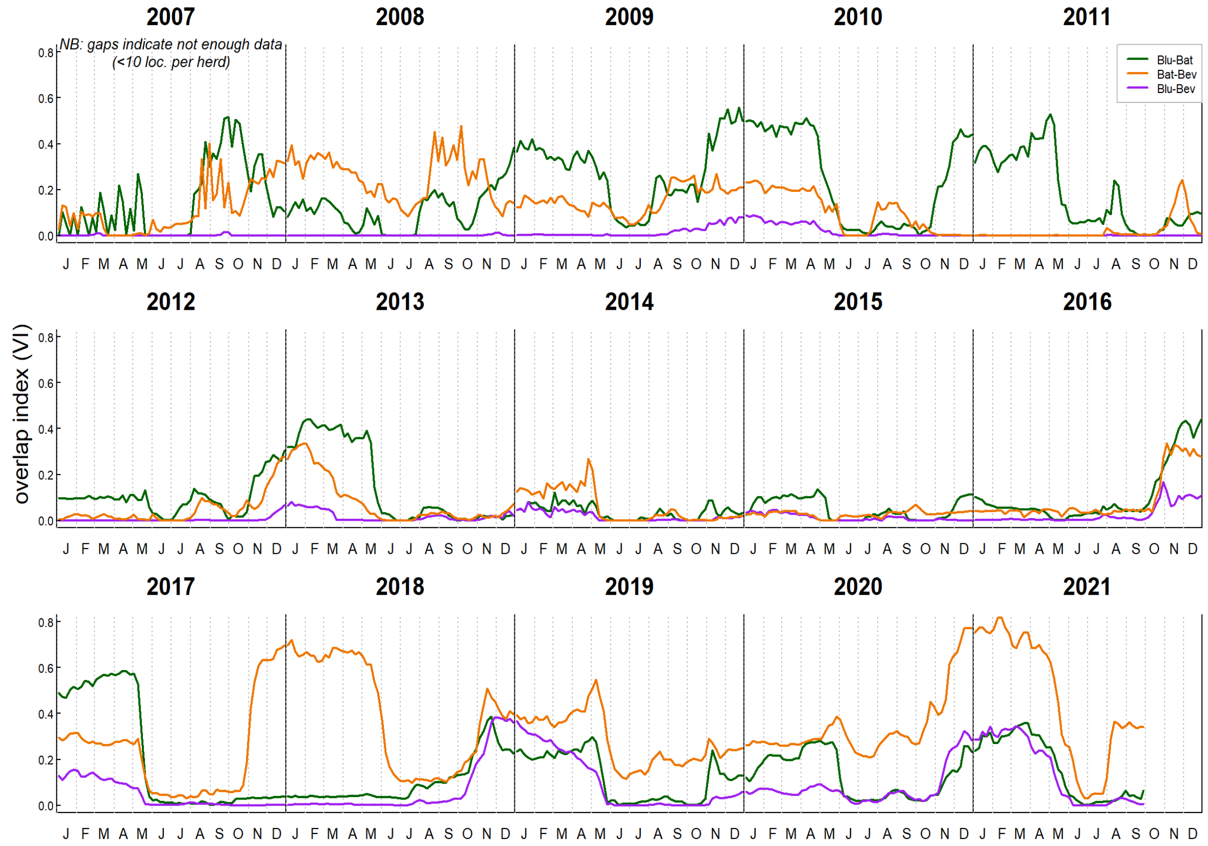

Figure 5. *Estimated mean VI overlap by 6-day period throughout the year for all years since 2006 for each of the three pairs: Bluenose East and Bathurst (Blu-Bat, red lines), Bathurst and Beverly (green lines) and Bluenose East and Beverly (blue lines).*

The aggregated results (Figure 6) also point to a two-stage increase in VI 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).

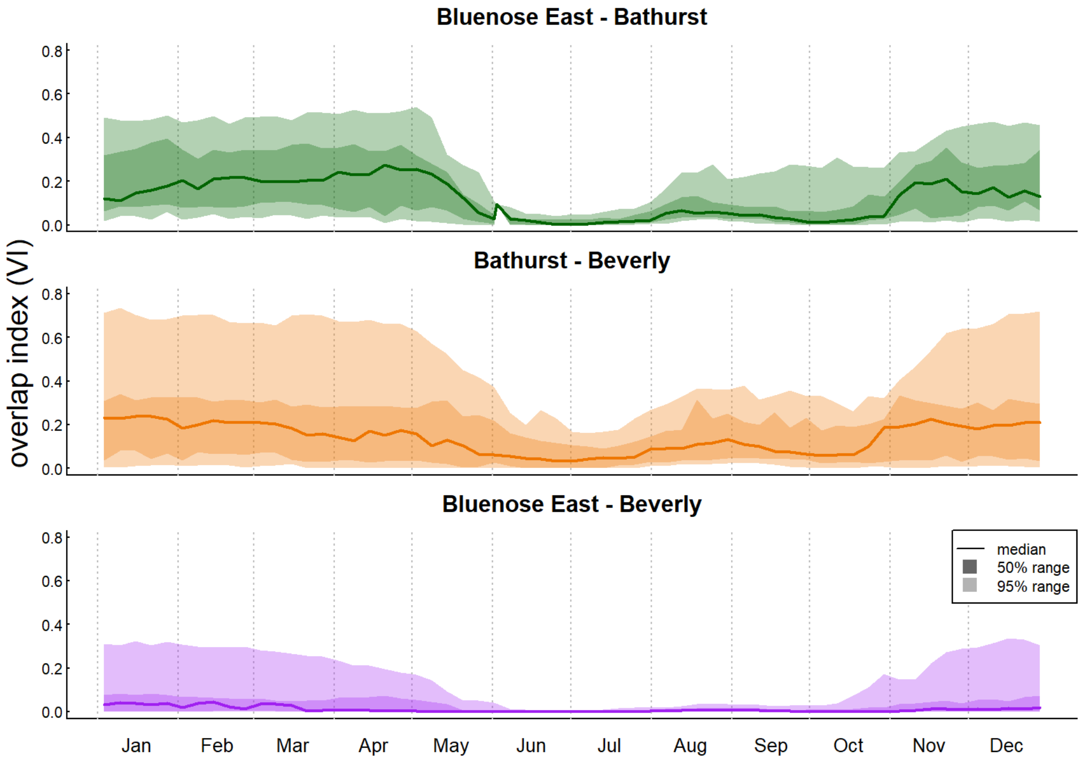

Figure 6. *Median, inter-quartile range (darker shading), and 95% range (lighter shading) of herd-level VI overlap estimates by 5-day period 2005-2021.*

In high VI overlap winters, the precise timing of the breakdown in VI overlap, corresponding to the separation of the herds for the pre-calving migration, is sharp and consistent (Figures 5, 6 & 7). For example, Blu-Bat overlap plummeted from over 0.40 to under 0.01 between mid-May and the end of May. These dates correspond to the rather sudden beginning of the pre-calving migration to the calving grounds. The ramp-up in VI overlap in the preceding fall was more gradual and varied more inter-annually (Figure 5, 6 & 7).

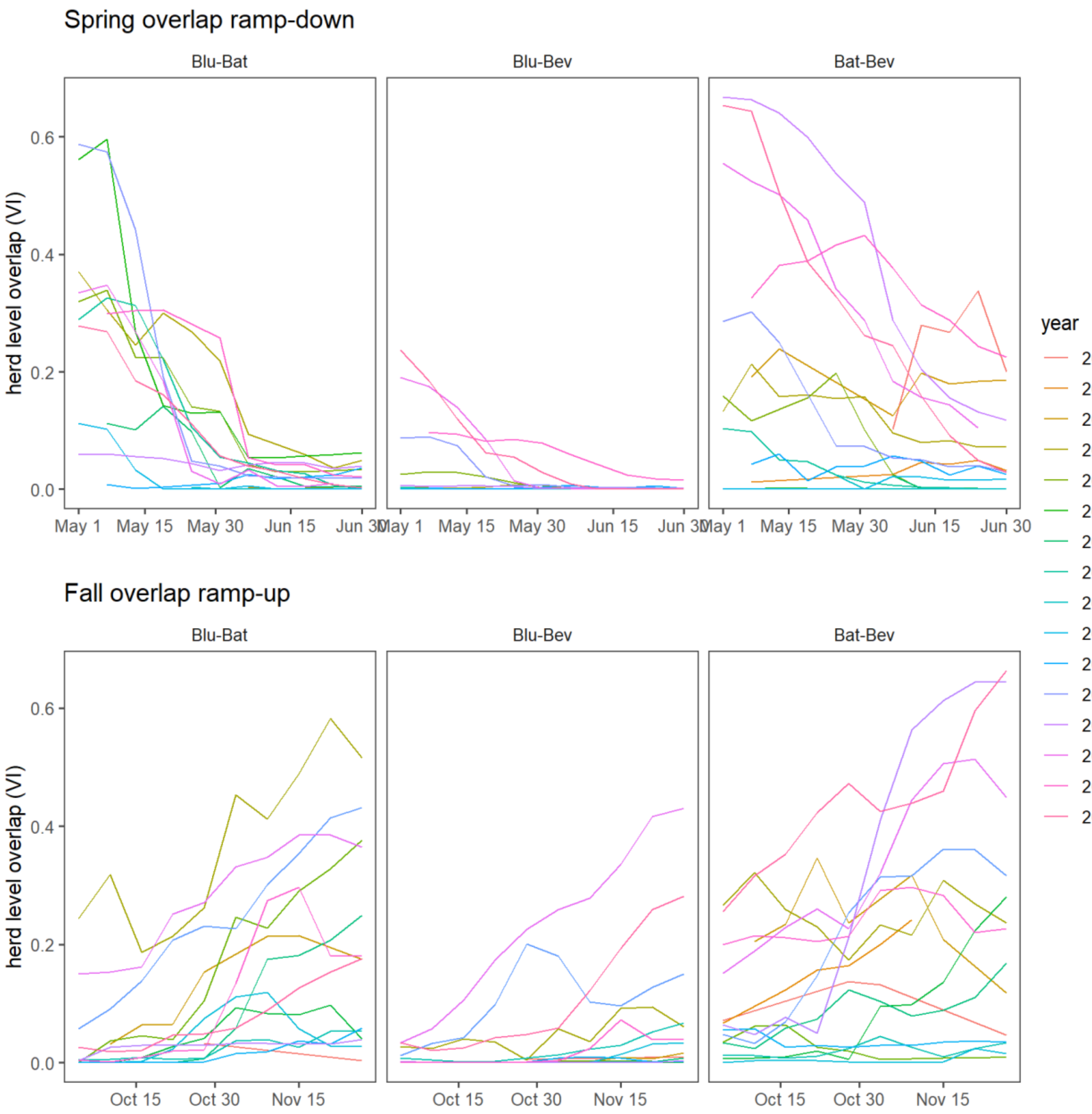

Figure 7. *Annual comparison for the herd VI overlap showing the spring 'ramp-down' and fall 'ramp-up' for the Bathurst herd with the Bluenose East and Beverly herds.*

3.3 Inter-individual distances

The number of encounters among individuals within the same herd (expressed as the Corrected Encounter Index) varied throughout the year and across years (Figure 8), even though this index sharply alters the relative height of the encounter peaks (Table 4, Figure 8), especially the high mid-summer insect aggregations in recent years for the Bathurst herd. The index was low during winter and increased during spring migration to very high values during summer in some years, reflecting a potential effect of insect harassment on caribou. Intense insect harassment may lead individuals to aggregate to reduce harassment per capita. The index was, overall, higher for Bathurst (mean 0.306, sd 0.87) followed by Beverly (0.081, sd 0.38) and Bluenose East (0.042, sd 0.10).

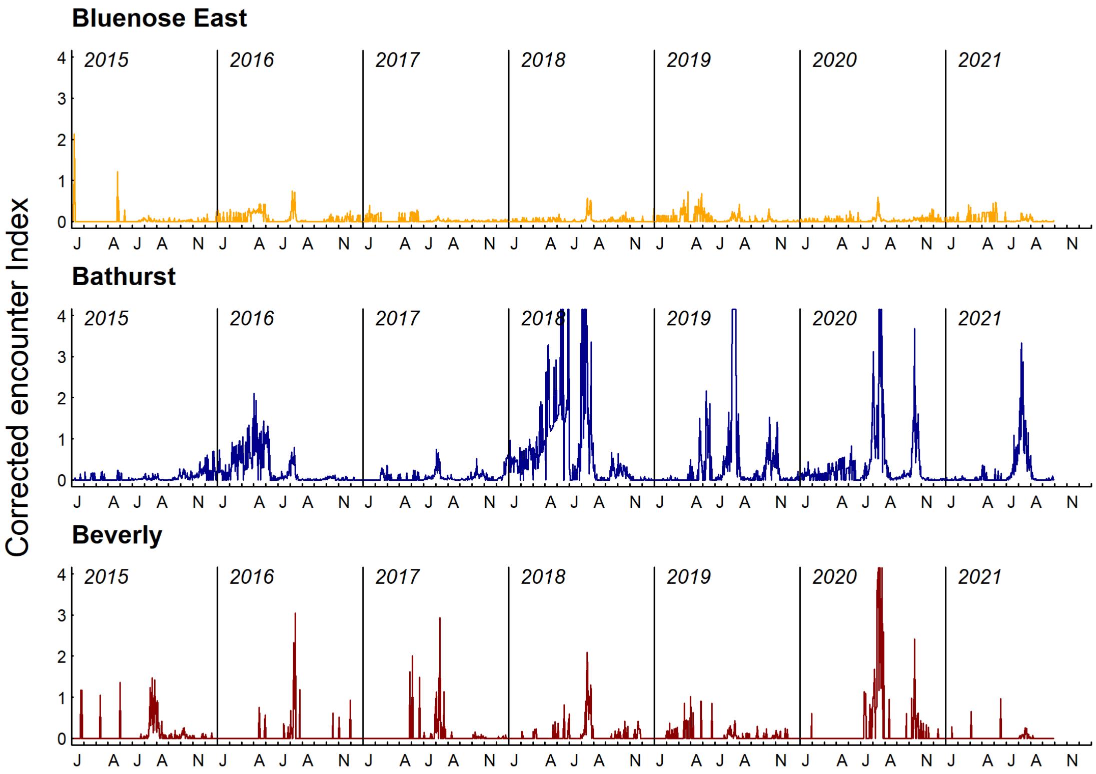

Figure 8. *Corrected encounter index, showing the number of encounters within herds, relative to a number of uniformly randomly-present individuals within an area the size of the 50% kernel of the animal locations of a given herd on a given day.*

Table 5. **Average number of daily encounters among herds by year and month.**

Blu-Bat							Bat-Bev						
2015	2016	2017	2018	2019	2020	2021	2015	2016	2017	2018	2019	2020	2021
0.00	0.00	0.23	0.00	0.03	0.00	0.03	0.00	0.13	0.03	0.10	0.10	0.10	0.19
0.00	0.00	0.25	0.00	0.07	0.00	0.14	0.04	0.04	0.00	0.29	0.25	0.10	0.32
0.16	0.00	0.32	0.00	0.00	0.03	0.16	0.00	0.00	0.00	0.19	0.32	0.45	0.42
0.10	0.00	0.50	0.00	0.03	0.00	0.07	0.00	0.14	0.03	0.20	0.53	0.10	0.43
0.00		0.10	0.00	0.08	0.00	0.00		0.12	0.06	0.10	0.03	0.03	0.00
0.00	0.03	0.00	0.00	0.00	0.00	0.00	0.20	1.00	1.50	0.60	0.00	2.77	0.00
0.00	0.55	0.00	0.26	0.00	0.00	0.00	0.77	0.90	2.90	3.84	0.39	15.71	0.29
0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.03	0.77	0.10	0.03	1.90	0.13
0.00	0.00	0.00	0.07	0.00	0.10	0.00	0.33	0.03	0.13	0.53	0.03	0.67	0.00
	0.32	0.00	0.10	0.00	1.00		0.58	0.39	0.90	1.13	0.81	7.23	
0.00	0.43	0.00	0.00	0.00	0.03		0.03	0.00	0.47	0.23	0.10	0.33	
0.00	0.06	0.00	0.10	0.10	0.06		0.00	0.00	0.13	0.19	0.06	0.16	

***Table 6.* 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	2014	2015	2016	2017	2018	2019	2020
Bluenose East	8 (18.94)	98 (33.01)	74 (35.23)	68 (31.34)	117 (40.61)	87 (35.02)	215 (43.62)
Bathurst	20 (12.97)	565 (30.14)	146 (30.60)	517 (27.33)	303 (25.91)	336 (25.77)	831 (42.35)
Beverly	4 (20.72)	49 (29.52)	6 (20.52)	50 (37.42)	49 (32.66)	17 (27.91)	28 (17.71)
Blu-Bat	8 (31.68)	0 (63.25)	67 (65.83)	0 (58.67)	12 (66.76)	4 (60.03)	46 (85.97)
Bat-Bev	1 (34.12)	31 (59.99)	16 (51.12)	72 (64.74)	85 (58.57)	54 (53.68)	280 (60.06)
Blu-Bev	0 (37.93)	0 (60.00)	0 (55.63)	0 (61.14)	4 (73.67)	0 (61.97)	12 (61.33)

The total number of encounters of individuals between herds (Tables 5 and 6) varied considerably across years. We counted 1,817 individual encounters across herds between 2014 and 2021 (168 Blu-Bat, 1,633 Bat-Bev, 16 Blu-Bev). In general, Bathurst and Beverly individuals had the most encounters and Bluenose East and Beverly had the least encounters every year.

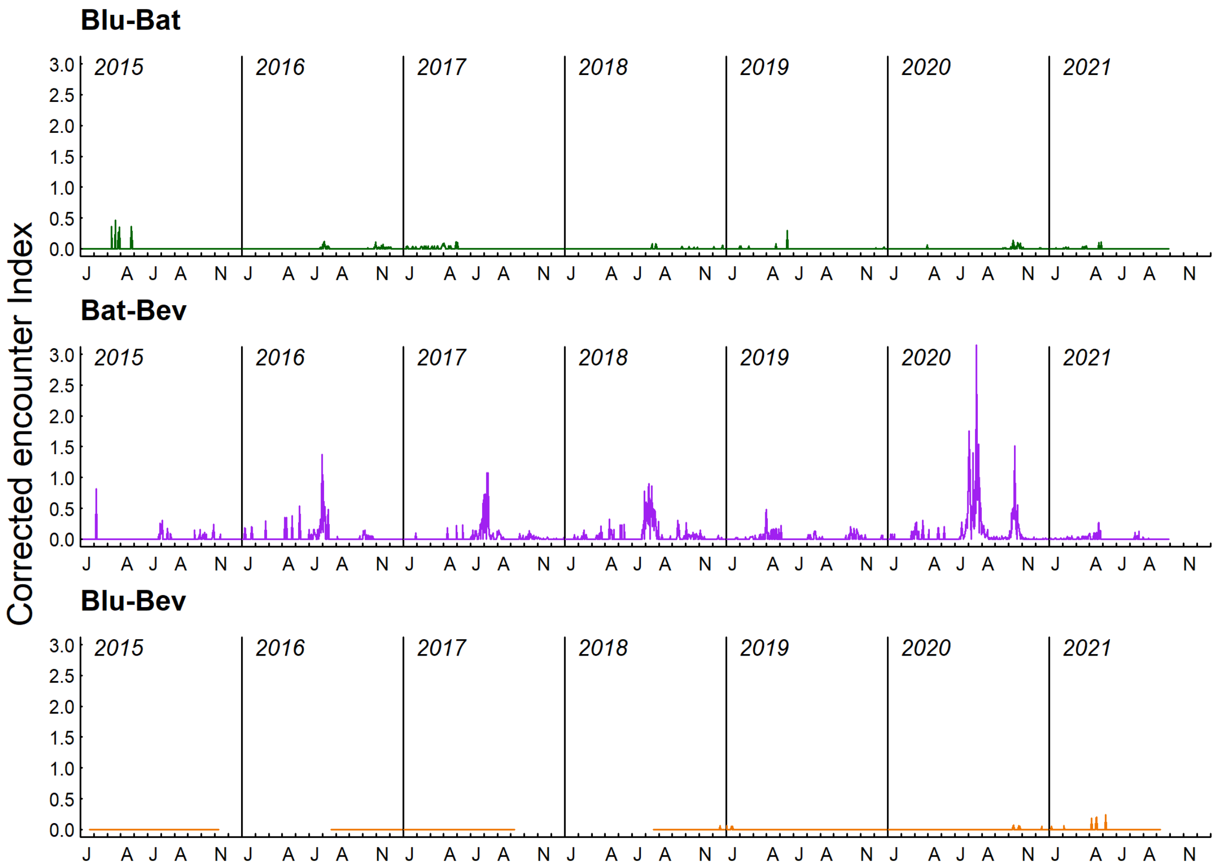

Figure 9. *Corrected encounter index, showing the number of encounters within 200 m of individual collared caribou across herds, relative to a number of uniformly randomly-present individuals within an area the size of the 50% kernel of the animal locations of a given pair of herds on a given day.*

We fit a generalized additive model (GAM) smoothed 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 2006). 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. There is 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 more recent years. In general - as noted above – the Bathurst herd, at extremely low numbers, tend to have higher aggregation indices than Bluenose East and Beverly animals.

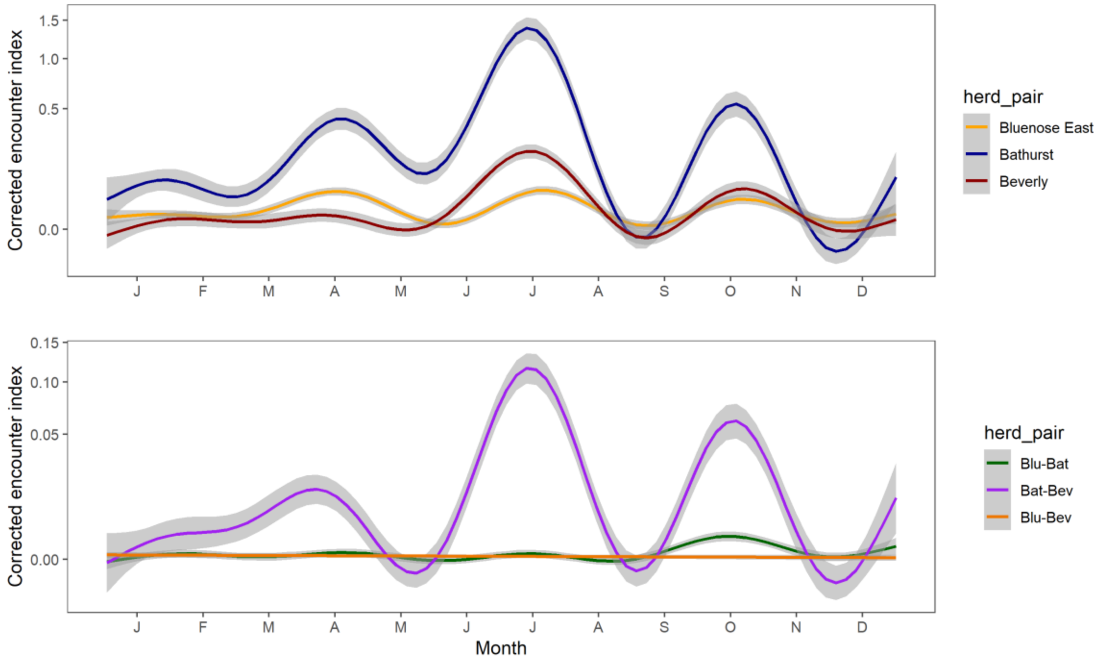

Figure 10. *Corrected 200 m encounter index within and between herds by day of year. The curve represents a Generalized Additive Model smooth wrapped around the beginning and end of the year; the shaded area is the 95% confidence interval. Note, the data are presented on a square-root transformation.*

4. 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 (2006-2021), overlap between the winter distribution of the Bathurst and Beverly 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, fall migration and rut can be discerned with a defined peak in pairwise distances. While annually variable, for the period 2014-2021 there is no trend in the timing of peak fall migration and rut compared to trends in the summer peak, which appears to be coming later in July. Note that 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.

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 herds. 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 Prichard 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.

Prichard et al. (2020) found a similar pattern of more overlap between neighboring herds in winter but aggregated their results for 2003-2015 rather than examining inter-annual variation.

At a finer scale (i.e., the individual scale), we examined within- and among-herd spacing relative to each other as a measure of encounters. 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 2006-2021 when sample sizes were adequate. Our selection of timescales of annual to 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 calving grounds (Adamczewski et al. 2019a; Adamczewski et al. 2019b). This emigration and a shift in calving distribution (Figure 11) are reflected in a higher overlap index for Bathurst and Beverly (Figure 8). The emigration may either be a consequence of overlapping winter distribution as a likely result of the shifting winter ranges for both herds (Adamczewski et al. 2019a), or a response to the continued decline and consequent low densities of cows on the Bathurst calving grounds (Adamczewski et al. 2015; Gunn, Poole, and Nishi 2012). The overlap between Bluenose East and Bathurst herd winter ranges did not result in emigration to either herd’s calving grounds (Adamczewski et al. 2019a).

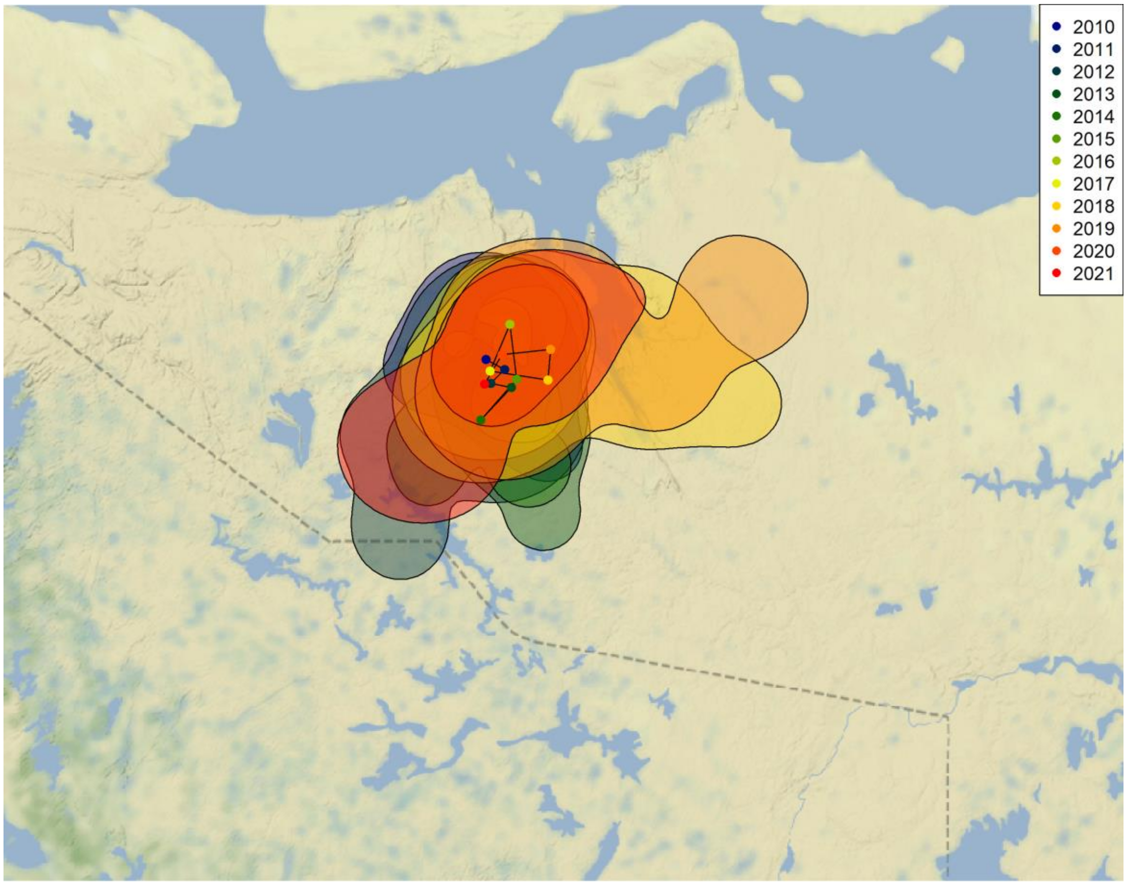

Figure 11. *Annual overlapping polygons (95% kernel) and centroids for the Bathurst herd calving grounds (Analysis developed by Couriot et al. In prep. applied to the Bathurst herd from 2010 to 2021, see https://ocouriot.github.io/IdentifyingCalvingGrounds.html).*

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. (2008) 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 overlap and encounter trends. The changing relationship between the Bathurst herd with its two neighboring herds occurs as the Bathurst and Beverly herds have continued to shrink and slightly shift their winter ranges. The Bathurst herd's winter range has slightly shifted east since 2016, while the Beverly herd's winter range shifted north and west (Figure 12), which coincides with the higher overlap we observed in the most recent years.

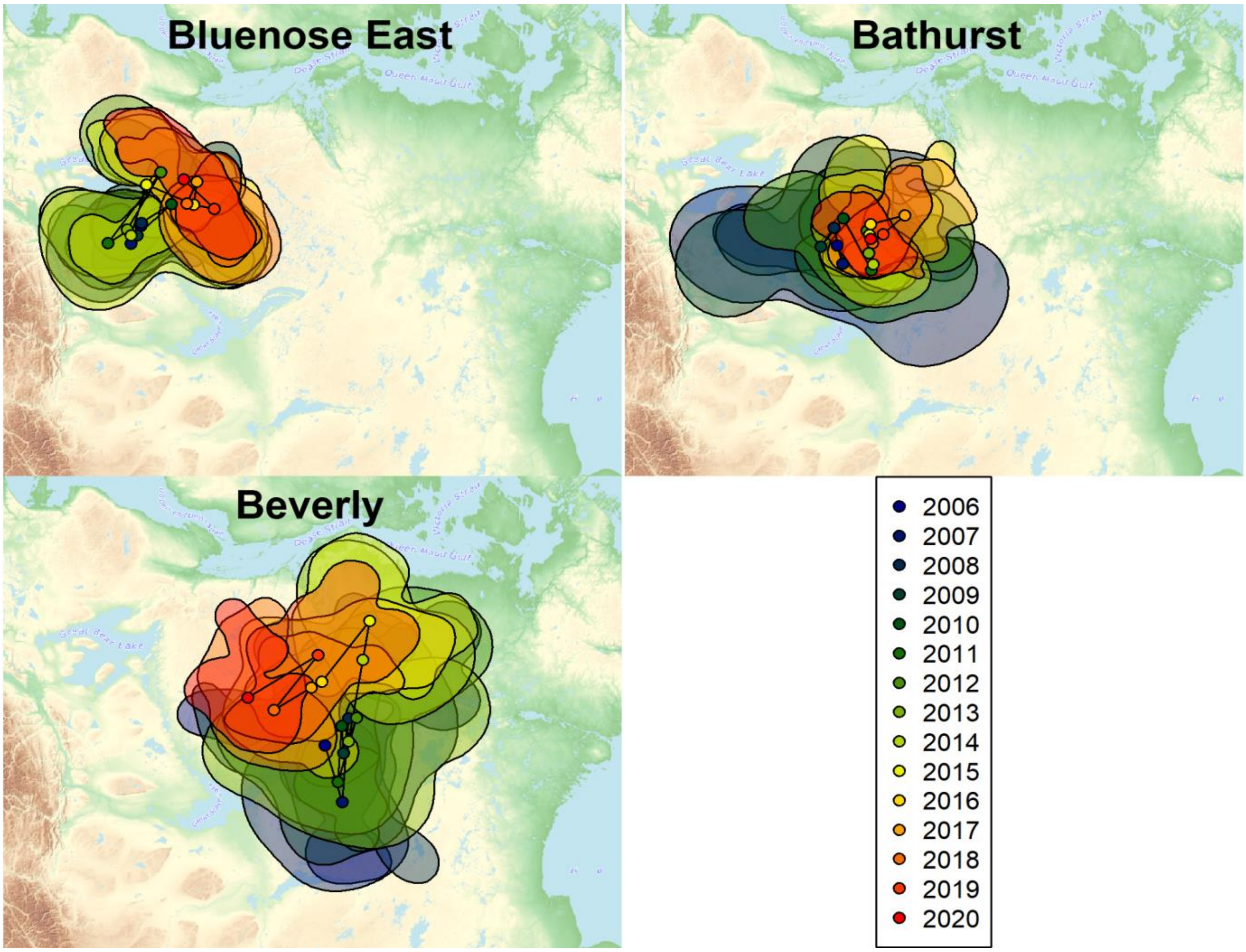

Figure 12. *Annual overlapping winter ranges (95% kernel) and centroids for Bluenose East, Bathurst and Beverly herds.*

The relationship between shifts in the Bathurst herd's winter ranges and neighboring herd winter ranges differs from what Le Corre et al. (2020) 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 the 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. However, 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 (Mennell 2021, Gunn 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. (A. Gunn).*

Interestingly, cross-herd encounters were relatively low even though 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 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). Group size during migration increases sharing of information and experience as and likely improves energetic efficiencies (Berdahl et al. 2016; Torney et al. 2018). Although the encounters between collared caribou from the Bluenose East and Bathurst herd were high in May 2017 and 2019, they did not result in calving ground switches (Boulanger et al. 2019). However, switches of Bathurst herd cows to the Beverly herd's calving ground in recent years (Adamczewski et al. 2019a) did coincide with the higher rate of cross-herd encounters. Both the Bathurst and Beverly migrate northeast from their winter to calving ranges and previously (2001 and 2002), collared cows shared initial pre-calving migratory pathways (Gunn and D'Hont 2002). It is possible that the combination of increased sociality between Bathurst and Beverly individuals and their shared initial spring migration routes has contributed to recent calving ground switches by Bathurst caribou.

Annually, tracking the extent and timing of overlap between neighboring herds is an essential contribution to assigning harvest quotas and predation rates, which are managed at the herd scale. Additionally, monitoring overlap and its timing can identify unexpected changes in herds' distribution, 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.

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