The Journal of Wildlife Management 84(8):1500–1514; 2020; DOI: 10.1002/jwmg.21934

Research Article

Interchange and Overlap Among Four Adjacent Arctic Caribou Herds

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ABSTRACT Barren ground caribou (*Rangifer tarandus granti*) are distributed in herds that seasonally use specific geographic regions within an annual range, with varying levels of fidelity during different periods (e.g., calving, insect relief, wintering). As a result, caribou management is generally tailored to individual herds that often range across administrative boundaries. Herd ranges can shift over time, seasonal ranges of adjacent herds often overlap, herds merge, and there is often little genetic differentiation among adjacent herds. If substantial herd interchange occurs, it would have important management implications by influencing estimates of herd size, herd composition, and harvest rates. We compiled satellite telemetry data from 2003–2015 for 4 large arctic caribou herds to quantify herd interchange rates. We calculated a metric of herd interchange based on the relationship of caribou locations to typical weekly herd ranges (all yrs combined) and the distance to other radio-collared caribou from each of the 4 herds (yr specific). Although herd membership cannot always be clearly defined based on location, this metric provides an objective measure of the strength of evidence of herd membership that can be used to make comparisons among herds and time periods. We also calculated herd overlap and quantified how it varied throughout the year. Herd interchange was rare in the 2 larger herds, generally occurring when caribou overwintered with an adjacent herd, whereas herd interchange from the 2 smaller herds was more frequent and could last longer than a year. Although sample sizes were limited, there were no clear patterns in herd interchange with year or annual herd size. The 2 smaller herds had large seasonal overlap with adjacent herds, suggesting that herd interchange may be related to spatiotemporal herd overlap and relative herd size. Our results can help managers understand herd interchange and overlap to make management decisions, interpret research results, and develop more accurate population models. © 2020 The Authors. The *Journal of Wildlife Management* published by Wiley Periodicals LLC on behalf of The Wildlife Society.

KEY WORDS Alaska, herd fidelity, kernel density estimation, meta-population, *Rangifer tarandus*, telemetry.

Management of wildlife species is often conducted over discrete geographic areas based on factors such as differences in habitat, animal densities, or political boundaries. The proper identification of management units is a central concern to the conservation of natural populations (Passbøll et al. 2006). In addition, information on genetics and demographic factors of groups are necessary for determining the minimum viable population sizes and other metrics important for management (Lande 1988). Assessing harvest levels or development effects on a population can be influenced by decisions about species population structure and the relevant management units (Taylor et al. 2000).

For species that form herds or other groups with distinct movement patterns and seasonal aggregations, analyzing location data from telemetry data or other sources is often necessary to define groups (Bethke et al. 1996, Nagy et al. 2011, Sinsch et al. 2012). In many cases, management at the herd level is logical and generally entails assuming the herd represents a closed population (Valkenburg et al. 2002). Success of this management strategy will depend, in part, on how consistent movement patterns are, and how much interchange and overlap occurs with adjacent herds. Large violations of the assumption of a closed population could result in biased estimates of important management metrics (e.g., herd growth rate, harvest rate). In addition to management implications, the degree of group interchange

Received: 4 April 2019; Accepted: 23 June 2020

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and overlap has important implications for genetics, species conservation, disease transmission, and vulnerability to change (Vors and Boyce 2009, Festa-Bianchet et al. 2011, Magle et al. 2013, Mager et al. 2014).

Barren ground caribou (*Rangifer tarandus granti*) occur in herds that exhibit specific patterns of annual movements including high fidelity to specific calving areas and typical patterns of distribution and movement for summer insect relief, seasonal migration, and wintering grounds (Skoog 1968). There can be considerable variability and shifting over time in these range use patterns (Davis et al. 1986, Hinkes et al. 2005). Seasonal use areas can move (Valkenburg and Davis 1986, Gunn et al. 2010), adjacent caribou herds can merge (Valkenburg et al. 1988; Hinkes et al. 2005; Young 2015*a*, *b*), and individuals or groups may make atypical movements (Adams et al. 2005). Many adjacent herds show little genetic differentiation (Zittlau et al. 2000, Roffler et al. 2012, Mager et al. 2014), and defining a herd may not always be simple. In Alaska, USA, caribou herds are typically delineated based on calving areas (Skoog 1968), but Hinkes et al. (2005:1157) noted that groups of caribou have been, at times, classified as "…main herds, major herds, minor herds, remnant herds, subherds, bands, off-shoots from other herds, relic herds, segments, satellite herds, peripheral groups, and subpopulations." Nevertheless, in practice, defining individual herds is a necessary concept for management purposes (Valkenburg 1998, Mager et al. 2014) because basic management and harvest statistics are determined based on a herd.

If individual caribou do move among herds in substantial numbers or with high frequency, quantifying the pattern of movements could improve caribou management, and provide greater insight into short-term versus long-term perspectives on the nature of caribou meta-populations and caribou ecology (Hinkes et al. 2005). Depending on the season in which inter-herd movements occur, they could add variability to estimates of population size, sex ratios, recruitment, survivorship, and harvest rates that are important to management. Any additional error in these metrics would then introduce errors into population models.

Previous studies by caribou biologists have noted instances of individual radio-collared caribou changing herds, and there have been some attempts to quantify this potentially important activity (Cameron et al. 1986, Davis et al. 1986, Boulet et al. 2007, Person et al. 2007, Roffler et al. 2012), but they were often hampered by limited data. The availability of long-term satellite-collar data sets for the 4 Alaskan caribou herds that calve in the Arctic provides a new opportunity to quantify inter-herd movements in a consistent manner over an extended time period.

We analyzed data from satellite radio-collars for 4 caribou herds to determine 1) how frequently individual caribou are associated with a different herd, 2) how rates of herd interchange vary among the herds, 3) if seasonal or annual patterns of interchange varied by herd, 4) how long movements to a different herd typically last, and 5) how much seasonal herd overlap occurs. Our goal was to understand and describe the magnitude and patterns of herd interchange and overlap because it may affect population management of these 4 caribou herds. Thus, we developed an objective metric of herd interchange to accomplish that goal for these herds.

STUDY AREA

Our study area encompasses movements of caribou during 2003–2015, in the ranges of the 4 caribou herds that calve in arctic Alaska: the Western Arctic Caribou Herd (WAH), the Teshekpuk Caribou Herd (TCH), the Central Arctic Herd (CAH), and the Porcupine Caribou Herd (PCH; Fig. 1). This area covers approximately 644,000 km^2, from western Alaska across the Arctic Coastal Plain and Brooks Range to the Yukon Territory, Canada. The area is largely undeveloped, with the exception of small communities, oil development, the Dalton Highway, and Trans-Alaska Pipeline System in the range of the CAH (Nicholson et al. 2016), the Dempster Highway in the PCH range (Johnson and Russell 2014), the Red Dog Mine and its road and port in the WAH range (Wilson et al. 2016), and some other small roads and development projects. Subsistence hunting for caribou is culturally and economically important for communities in the area (Condon et al. 1995, Titus et al. 2009).

The area is predominantly compromised of arctic tundra within the coastal plain, alpine tundra in the Brooks Range, and taiga in the southern portions of the study area. The elevation varies from sea level along the Chukchi and Beaufort Sea coasts to mountain peaks >2,000 m in the Brooks Range. The summers (Jun–Aug) are cool and winters (Nov–Apr) are long and cold. Between 1981 and 2010, the mean temperature in July (the warmest month) was 8.0°C, the mean temperature in February (the coldest month) was −27.2°C, and the annual precipitation was 102.6 mm, with approximately 70% of precipitation occurring June–September, in Prudhoe Bay (70°19′32″N 148°42′41″W), near the central portion of the study area (http://climate.gi.alaska.edu/acis_data, accessed 24 Mar 2020). The major predators of caribou adults or calves include grizzly bears (*Ursus arctos*), wolves (*Canis lupus*), golden eagles (*Aquila chrysaetos*), and wolverines (*Gulo gulo*; Whitten et al. 1992, Murphy and Lawhead 2000).

These 4 herds show strong fidelity to specific calving ranges but have wide overlap in annual herd ranges (Fig. 1). Thus, genetic analysis has indicated that there is widespread gene flow among the herds (Mager et al. 2014). These herds also vary widely in population size, trends, and in some life-history strategies (Person et al. 2007, Caikoski 2015, Nicholson et al. 2016, Joly and Cameron 2017). Calving typically occurs in late May or early June, insects are a dominant factor influencing behavior from late June to mid-August, and rut takes place in October.

The WAH is primarily in northwestern Alaska, and their herd range extends from the central Seward Peninsula along the coast to Utqiaġvik including the Arctic Coastal Plain to the western and central Brooks Range (Fig. 1). The WAH calves in the Utukok Uplands in the northwestern foothills of the Brooks Range, and then moves through the western Brooks Range during midsummer when insect harassment occurs. The herd typically winters in western Alaska, with most caribou on or east of the Seward Peninsula during this

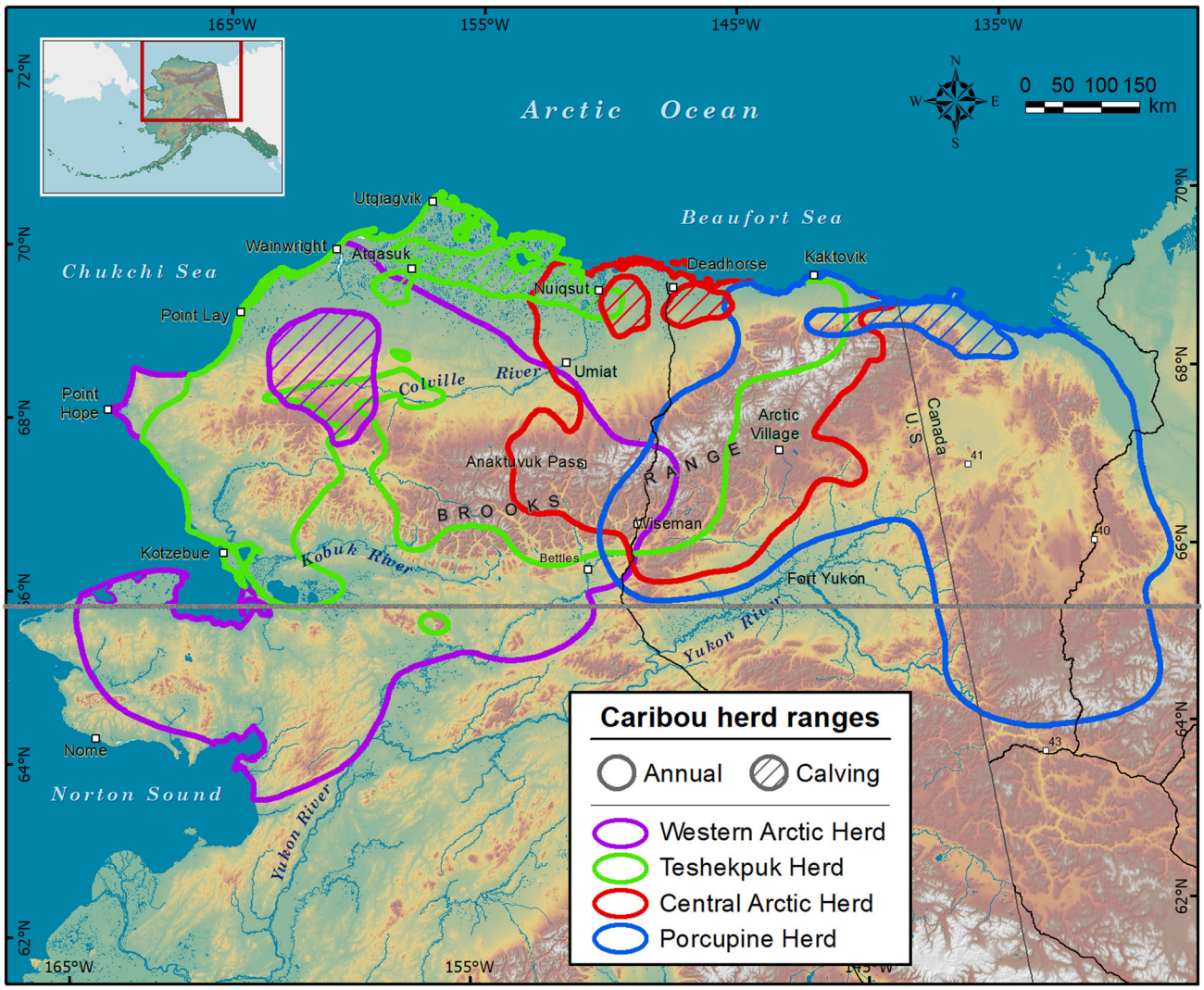

Figure 1. The calving and annual herd ranges, calculated from kernel density estimation of female caribou locations, of 4 arctic herds in northern Alaska, USA, or Yukon Territories, Canada, 2003–2015. Calving ranges are calculated based on all radio-collared female caribou during calving.

study. The WAH reached a recent peak size of 490,000 caribou in 2003 but was estimated at 259,000 caribou in 2017 (Table S1, available online in Supporting Information; Dau 2015, Hansen 2018). Adult caribou in the WAH were collared by boat when they crossed the Kobuk River during fall migration; animals were not re-collared (Dau 2015).

The core range of the TCH is on the central Arctic Coastal Plain (Fig. 1). The highest density calving occurs near Teshekpuk Lake and the primary insect-relief habitat area is between Teshekpuk Lake and the Beaufort Sea coast (Kelleyhouse 2001, Parrett 2007, Person et al. 2007, Wilson et al. 2012). The TCH has 2 main wintering strategies, with most animals remaining on the Arctic Coastal Plain during winter, but many animals, including a disproportionate number of males, wintering in the central Brooks Range or less frequently in the western Brooks Range (Carroll et al. 2007, Person et al. 2007, Parrett 2015). The TCH grew from a population of about 5,000 in the late 1970s, when it was first identified as a separate herd, to a peak of 69,000 animals in 2008 (Parrett 2015). The most recent photo-census conducted in 2017 indicated a population of 56,000 animals (Table S1; Parrett 2015, Klimstra 2018). Caribou in the TCH were collared during late June or early July using a net-gun fired from a helicopter. Some caribou were re-collared multiple times (Parrett 2015).

The CAH calves in 2 distinct calving areas: between the Colville and Kuparuk rivers on the west side of the Sagavanirktok River (with highest densities typically occurring south of the Kuparuk oilfield) and between the Sagavanirktok and the Canning Rivers, east of the Prudhoe Bay oilfield (Murphy and Lawhead 2000, Wolfe 2000, Arthur and Del Vecchio 2009, Nicholson et al. 2016). The CAH uses the Beaufort Sea coast for primary insect-relief habitat and winters in or near the east-central Brooks Range (Fig. 1). The CAH grew from approximately 5,000 animals in the mid-1970s, when it was first identified as a separate herd, to a peak of 68,000 in 2010, but then declined to 23,000 in 2016, and was estimated at 28,000 animals in 2017 (Table S1; Lenart 2015, 2018). Most caribou in the CAH were collared near the Brooks Range in spring at 9–10 months old, but some were collared near the coast in early summer. Some caribou were re-collared multiple times (Lenart 2015).

The PCH typically calves in the northeastern corner of Alaska in the Arctic National Wildlife Refuge (ANWR) and in the adjacent Yukon Territories (Fig. 1; Russell et al. 1993, Griffith et al. 2002, Caikoski 2015). The PCH uses ridgetops in the eastern Brooks Range for their primary insect-relief habitat (Walsh et al. 1992) and winters in the western Yukon Territories and the central and eastern Brooks Range in Alaska (Russell et al. 1993, Caikoski 2015). The PCH numbered approximately 178,000 in 1989, declined to approximately 123,000 in 2001, and has increased in recent years to an estimated population size of 218,000 in 2017 (Table S1; Caikoski 2015, 2018). Most caribou in the PCH were collared at 9 months of age in March on the wintering range in the Brooks Range. Some caribou were re-collared multiple times (Caikoski 2015).

METHODS

We compiled data from platform terminal transmitter (PTT) and global positioning system (GPS)-collars that had been deployed on female caribou in the WAH, TCH, CAH, and PCH from 2003–2015. Procedures for handling live animals conformed to guidelines of the American Society of Mammologists (Sikes and Gannon 2011) and were approved by the Alaska Department of Fish and Game (ADFG) Animal Care and Use Committee (approval numbers ADFG-0018, ADFG-0019, ADFG-0035, and ADFG-0040). The majority of available radio-collars were deployed on females because of the importance of documenting calving location and success and the difficulty of outfitting male ungulates with GPS collars (Dick et al. 2013). We therefore confined our analysis to the behavior and movements of female caribou. Caribou exhibit different degrees of sexual segregation during different seasons; therefore, the results from radio-collared females may not apply to males during all seasons. To examine seasonal differences in inter-herd movements, we summarized the data by different months or groups of months (Nov–Apr, May, Jun, July, Aug, Sep, Oct). Although the timing varies somewhat by herd and year, these months roughly correspond to caribou seasons based on life-history events or weather conditions (Russell et al. 1993): spring migration largely occurs in May, most calving occurs in June, most insect harassment occurs in July, August provides a hiatus between insect harassment and snowfall, fall migration largely occurs in September and October, and rut occurs in October.

We used data sets that had previously been screened for erroneous locations by data managers. This screening varied somewhat among herds and data types (PTT, GPS) but included removing locations for poor-quality locations (e.g., by Argos location class for PTT data) and for erroneous locations based on distance-rate-angle filters (Prichard et al. 2014). After initial screening, we selected 1 location/week for each animal by selecting the location nearest the midpoint of the weekly period. We used only 1 location/week because we were interested in large changes in distribution that could adequately be described by weekly data. Because all collaring of caribou in the WAH occurred at a single location in fall, we removed all locations between the time of capture and the following June to account for the possibility that the movements of these radio-collared caribou were not representative of the entire herd during the first winter following capture. We also removed locations within 2 weeks of the initial capture for other herds although we expected their capture locations to be more representative of the distribution of the entire herd.

Herd Interchange

We used weekly caribou locations to calculate a metric of herd interchange based on the herd distributions, calculated by kernel density estimation (KDE), for each herd for each 7-day period during the year (all yrs combined) and the distance to adjacent radio-collared caribou from each herd (yr specific). Our final herd designation was based on mean values of this metric over ≥4 weeks; therefore, our use of the term herd interchange refers to a caribou that exhibits a pattern of movement that is typical of another herd for ≥4 weeks at any time of year. An interchange event lasts until there is evidence that the caribou has returned to the initial herd or moved to another herd (Table 1).

We assigned each caribou in this data set to the herd we presumed it to be a part of at the time of capture (initial herd); however, to ensure we assigned caribou to the proper initial herd, we examined the location of caribou during the first calving season after capture. If the animal was with a different herd during the first calving season following capture, we examined its entire track to determine the best initial herd assignment based on the timing and location of capture and a visual inspection of the animal's subsequent movement path.

For each individual caribou location, we calculated a metric of herd interchange (MHI) based on 2 components: a herd

Table 1. Definitions of measures and metrics used in this study of 4 Arctic caribou herds in northern Alaska, USA, and Yukon Territories, Canada, 2003–2015.

Measure	Metric	Definition
Herd interchange		A caribou that is determined to most likely be on the range of another herd for ≥4 weeks based on metrics calculated from weekly herd ranges and distance to other radio-collared caribou.
	Herd range component (HRC)	Metric indicating the strength of evidence for caribou being with another herd based on weekly herd ranges.
	Adjacent caribou component (ACC)	Metric indicating the strength of evidence for caribou being with another herd based on the distance to other radio-collared caribou of other herds.
	Metric of herd interchange (MHI)	Metric combining both HRC and the ACC to assess strength of evidence for being with another herd during a week.
Herd overlap		The proportion of other herds predicted to be in the main range (defined as the 75% isopleth) of a herd. Calculated on a weekly basis using kernel density estimation.

range component (HRC) and an adjacent caribou component (ACC). To calculate HRC we first calculated weekly ranges for each herd. For each week of the year (all yrs combined), we calculated a utilization distribution (UD) surface using KDE for each herd. We conducted the KDE using the plug-in method to estimate the smoothing parameter using the ks package for R (R Core Team 2017, Duong 2018). We clipped out the portions of the UD surface that were in the ocean or in Teshekpuk Lake (the largest lake on the North Slope of Alaska) but included locations <1 km from shore because some locations could be in the water near the coast owing to small location error or actual use of sea ice or shallow areas. We also included pixels on the sea ice of Kotzebue Sound that were used by caribou during migratory movements. We then converted those UD values for each herd to density contour isopleth values by calculating the sum of the pixels with higher UD values; these values indicate whether the caribou is in a high-density area for that herd (isopleth value close to zero) or a low-density area for that herd (isopleth value close to 1) for that week. We then calculated HRC values for each caribou location; HRC calculates the relative probability of membership in herd A relative to herd B by comparing isopleth values for 2 herds, using the following logit formula:

$$1 - \left[\frac{\left(\frac{\mathrm{iso_A} \times (1 - \mathrm{iso_B})}{\mathrm{iso_B} \times (1 - \mathrm{iso_A})} \right)}{1 + \left(\frac{\mathrm{iso_A} \times (1 - \mathrm{iso_B})}{\mathrm{iso_B} \times (1 - \mathrm{iso_A})} \right)} \right]$$

where $\mathrm{iso_A}$ is the isopleth value for herd A, and $\mathrm{iso_B}$ is the isopleth value for herd B. For each caribou location, we calculated HRC for each caribou location for the initial herd versus each of the other 3 herds during that week.

This formula produces a symmetrical range-based comparison of 2 proportions that estimates the probability of herd association. Values near 1 indicate a high probability of being with the initial herd (herd A) and values near zero indicate a low probability of being with the initial herd relative to an alternate herd (herd B).

To calculate the ACC component for each caribou location we calculated the distance of nearest caribou from each herd for each week during each year. We calculated this component based on the mean distance of the nearest 20% of radio-collared caribou from each herd. We used a percentage of collars to avoid potential biases due to differing numbers of collars deployed on different herds. We used this percentage to ensure we used an adequate number of collars in the calculation while also accounting for herds that were distributed over large areas or in discrete groups. We calculated the ACC using the following equation:

$$\frac{\text{collar distance}_\mathrm{B}}{\text{collar distance}_\mathrm{A} + \text{collar distance}_\mathrm{B}}$$

where collar $\text{distance}_\mathrm{B}$ is the mean collar distance for the alternate herd and collar $\text{distance}_\mathrm{A}$ is the mean collar distance for the initial herd. Values near 1 indicate a high probability of being with the initial herd and values near zero indicate a low probability of being with the initial herd relative to the alternate herd. If either herd had <10 radio-collars active during a week, we did not calculate this component. We calculated an ACC of the herd change metric for each caribou location to account for annual variability in herd distribution among herds that was not captured by the HRC component and because large segments of a caribou herd can occasionally make atypical movements into the range of adjacent herds (Person et al. 2007, Bieniek et al. 2018).

We calculated MHI as the mean of the HRC and ACC, with each component receiving equal weight. The final MHI values varied between zero and 1, with values near zero indicating a high probability of being with another herd. Each weekly caribou location had 3 MHI values, one for each alternate herd. We used the minimum value, representing the most likely herd change, in subsequent calculations. We examined the effect of weighting the HRC and ACC components differently (Table S2, available online in Supporting Information).

We used calculations of weekly KDE maps to display the typical pattern of distribution for the herds, but some caribou had switched herds and were assigned to an incorrect herd prior to calculating the KDE surfaces. To minimize the effect of this potential error, we first ran our herd interchange analysis and calculated the MHI to identify caribou locations whose current herd assignment was questionable ($\mathrm{MHI} < 0.15$). We then temporarily assigned these caribou locations as unknown herd, and then recalculated the KDE maps without these caribou. We repeated this process twice to remove most caribou locations whose current herd assignment was questionable using the updated KDE surfaces. We identified 2.5% and 3.0% of locations as unknown using this process on the first and second iteration, respectively.

After calculating a weekly MHI, we examined the pattern of successive weekly values for each individual caribou to identify periods of herd interchange. For each caribou, we used change point analysis using the package ecp for R (James and Matteson 2014) to divide an individual's minimum MHI value for each week into distinct segments of time with similar values. We set the minimum duration for each segment at 4 weeks (e.g., each time period had similar values for this metric for a minimum length of 4 weeks) and we then calculated the mean value for each segment of time. We then set cut points for using these segment means to assign caribou to different herds based on visual inspection of movement data and typical patterns of seasonal herd distribution.

If an individual had a mean MHI value below our cut point of 0.2 during a time segment (min. time of 4 weeks), we assigned that caribou to another herd. If the mean MHI was <0.2 for >1 herd, we assigned the caribou to the herd with the smallest mean MHI. Once a caribou was determined to switch to an alternate herd, we assumed that caribou remained with that herd until the mean herd change metric rose above a high cut point of 0.7, indicating that the caribou returned to the initial herd again, or until the caribou switched to a different alternate herd. In this way, time periods for which there is no strong evidence of herd affiliation (herd change metric between 0.2 and 0.7) are

assigned to the herd with the most recent evidence of affiliation or the initial herd if no evidence of herd interchange is present. We set these cut points to have a stronger strength of evidence threshold for joining a new herd compared to returning to the initial herd, reflecting that movements with another herd are generally temporary. We acknowledge that these cut points are subjective; however, using numerical metrics to assign herd membership allows for comparisons among herds and time periods. We examined how choosing different cut points would change the results (Table S3, available online in Supporting Information).

For comparison with other studies, we also determined how many female caribou were with another herd during the calving period. We first identified the caribou assigned to other herds during the first week of June based on our herd change analysis. Because some caribou could be in the process of returning to their initial herd, we also plotted the movement path of each of these caribou to visually confirm that the movement path indicated the herd assignment based on the MHI during calving.

Because our radio-collar data was right-censored by mortalities, collar retrieval, or collar failure, we used Kaplan-Meier tests (Kaplan and Meier 1958) to compare the probability of inter-herd movements among the 4 herds. We tested for differences in the rate of inter-herd movements among herds and for differences in the rate of returning to the initial herd following being assigned to an alternate herd among herds using the survfit function in the package survival for R (Therneau and Grambsch 2000).

To test for linear changes in herd interchange over the years of our study, we determined if each caribou in the study had changed herds, based on our MHI values, during the year, we then ran a logistic regression of those results (changed or did not change herds) with year as an explanatory value. We used the log of the number of weeks of data available for each animal as an offset term to account for variability in duration of collaring among individuals and ran a separate analysis for each herd.

Herd Overlap

To examine the timing and extent of herd overlap in relation to inter-herd movements, we calculated the proportion of the UD of each of the other 3 herds within the 75% isopleth of a given herd on a given week (all yrs combined). This provides a metric of how much overlap typically existed in each herd range throughout the year, where overlap is defined based on the proportion of animals from adjacent herds rather than just area. We used the 75% isopleth as a delineation of the area that typically has moderate or high densities of caribou for a herd. High levels of herd overlap make it more difficult to identify herd interchange events and may result in higher levels of herd interchange.

We also used these results to calculate the proportion of caribou within a herd's weekly 75% isopleth that would be expected to be from a different herd by multiplying the proportion of each herd expected to be within another herd's weekly 75% isopleth by the mean herd size over the study period. Based on estimates of herd sizes over this period (Table S1; Caikoski 2015, Dau 2015, Lenart 2015, Parrett 2015), we used herd sizes of 348,000 for the WAH, 55,000 for the TCH, 54,000 for the CAH, and 188,000 for the PCH.

RESULTS

After screening, we compiled 58,608 weekly caribou locations from the 4 herds. Of all locations, 36.4% were from the WAH, 26.6% from the TCH, 21.0% from the CAH, and 16.1% from the PCH (Table S4, available online in Supporting Information). The mean number of female caribou locations (all yrs combined) used to calculate weekly kernel densities was 410 for the WAH (range = 336–536), 300 for the TCH (range = 246–356), 236 for the CAH (range = 186–265), and 181 for the PCH (range = 146–241). The mean number of years of data available for each caribou ranged from 1.74 for the WAH to 2.13 for the TCH (Table S5, available online in Supporting Information).

Herd Interchange

Using the MHI and cut points of 0.20 and 0.70 appeared to work well to identify herd interchanges. The correlation between the minimum estimates of HRC and ACC for all locations with adequate collar data available from all herds to calculate ACC was moderately strong ($r = 0.742$). Locations identified as being with an alternate herd were generally outside the typical distribution of the initial herd for a given time period (Fig. 2; Figs. S1–S3, available online in Supporting Information). A small proportion of caribou locations appeared to be clearly outside the typical herd distribution but did not have low herd interchange values, but some of these cases could be explained by situations where large groups from 1 herd made unusual movements to another area. One example of an unusual herd movement occurred when a large portion of the TCH went to the northeastern coastal areas of Alaska during winter 2003–2004 (Bieniek et al. 2018). These locations were correctly identified as remaining with the TCH (Fig. 1). One situation where the model had difficulty was distinguishing between CAH and PCH on winter range (Figs. S2–S3). Because of the large herd overlap during that season, a small change in geographic location could result in a caribou from CAH being assigned to the PCH.

The percentage of caribou locations assigned to other herds ranged between 0.9% and 8.7% for females of the 4 herds (Table 2). The highest rates of inter-herd movements for females were for the 2 smaller herds (TCH = 6.8%, CAH = 8.7%). Most of the movements were to adjacent herds, with little movement to non-adjacent herds (e.g., WAH to CAH or PCH). The proportion of females assigned to non-adjacent herds was zero for WAH and PCH, 0.1% for TCH to PCH, and 1.0% for CAH to WAH (Table 2).

Although sample sizes were limited, there were large differences in inter-herd movements by month and by herd. Most instances of caribou in the WAH being in the range

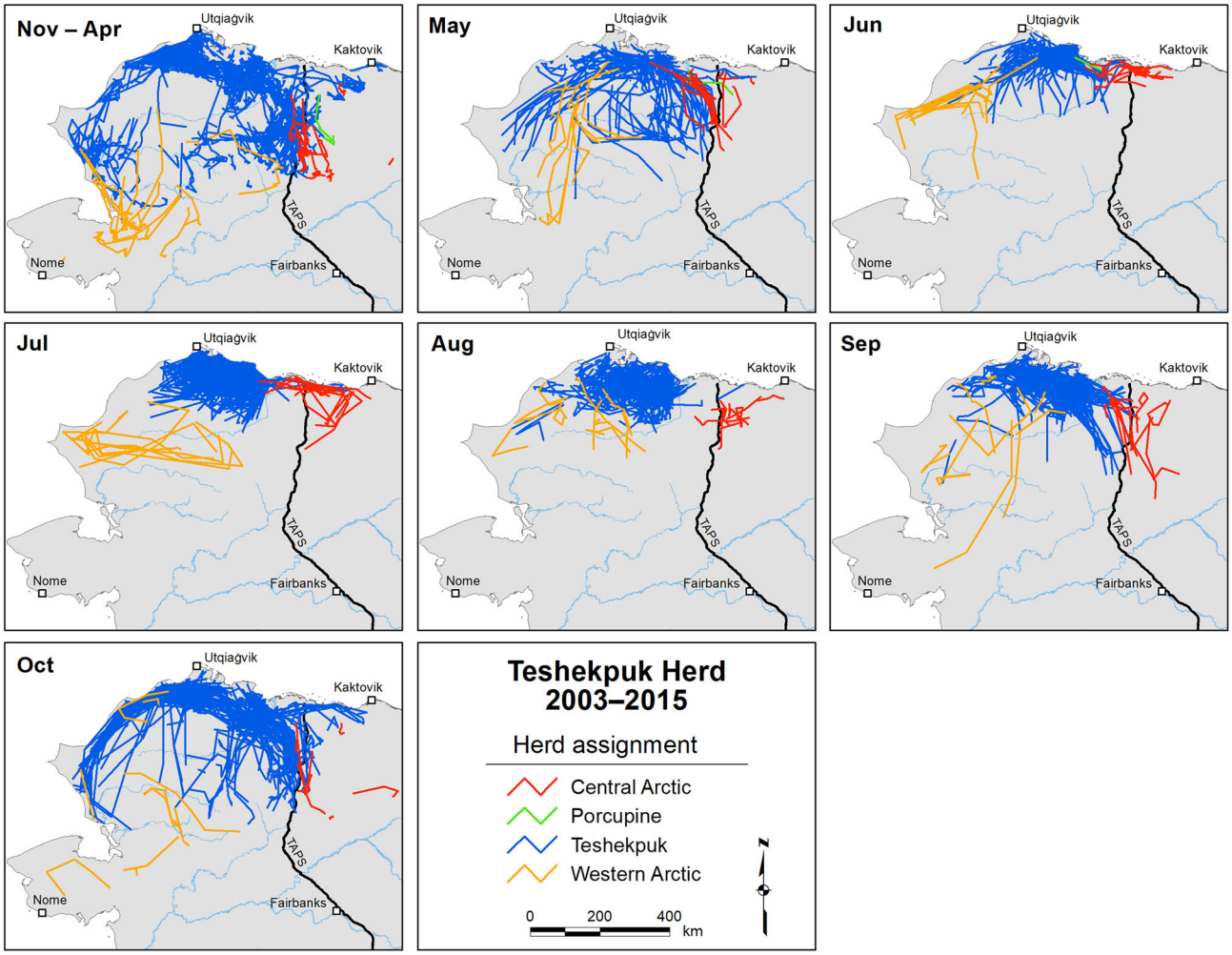

Figure 2. Distribution of female caribou initially with the Teshekpuk Herd by month and new herd designation, northern Alaska, USA, 2003–2015.

of other herds occurred during winter, and none occurred during July–August (Table 2). Some caribou in the TCH were in the WAH and CAH ranges during all time periods, but the highest rates occurred in May and June when >8% of locations were assigned to other herd ranges. For caribou in the CAH, the lowest percentages of locations assigned to other herd ranges occurred in May and June, and percentages were >6% in all other time periods, with the highest rate occurring during winter, although the rates for the CAH during winter may be somewhat inflated by the difficulties associated with high overlap with the PCH during that season. Caribou in the PCH had low percentages of locations in other herd ranges during all time periods, but the highest percentages for the PCH occurred in July and September–October, although they were still ≤1.2% (Table 2).

The mean annual percentages of caribou locations with other herds (Table 3) did increase with year for the CAH ($\beta = 0.132 \pm 0.036$ [SE], $P < 0.001$), and the PCH ($\beta = 0.312 \pm 0.153$, $P = 0.042$) but not for the WAH ($\beta = 0.121 \pm 0.079$, $P = 0.126$) or the TCH ($\beta = -0.001 \pm 0.044$, $P = 0.984$). For the CAH, the relationship was largely influenced by high values in 4 of the last 5 years. The PCH did not have any locations in other herd ranges during the first 7 years of data and then had consistently low rates after 2010 (Table 3). This change could reflect higher range overlap between the CAH and PCH in the later years of the study.

Although sample sizes were limited, there was some indication that the timing of the start of herd interchange varied by month among herds (Table 4). All WAH herd changes occurred in September–December when some WAH individuals were assigned to the TCH during the winter. The timing of herd change occurrences for the TCH was distributed over different months, except that no herd interchange events began in February or March. For the CAH, the highest percentages of herd interchange events began during July and October, but December through February also had multiple events occurring. The highest percentages of herd interchange events began in July for the PCH (Table 4), but few events occurred in any month.

The rates of herd interchange for female caribou differed ($\chi^2_3 = 41.1$, $P < 0.001$) among herds with higher rates for the TCH and CAH, than for the WAH and PCH (Fig. 3). The rate of herd interchange for the WAH was lower than

Table 2. Percentage of all weekly female caribou locations determined to be in other herd ranges by month and initial herd, northern Alaska, USA, and Yukon Territories, Canada, 2003–2015.

			New herd				
Initial herd	**Time period**	***n***	**Western Arctic**	**Teshekpuk**	**Central Arctic**	**Porcupine**	**Total**
Western Arctic	Nov–Apr	9,372		2.7	0.0	0.0	2.7
	May	1,467		2.0	0.0	0.0	2.0
	Jun	2,136		0.1	0.0	0.0	0.1
	Jul	2,376		0.0	0.0	0.0	0.0
	Aug	1,944		0.0	0.0	0.0	0.0
	Sep	2,092		0.3	0.0	0.0	0.3
	Oct	1,924		1.2	0.0	0.0	1.2
	Total	21,311		1.5	0.0	0.0	1.5
Teshekpuk	Nov–Apr	7,545	3.2		3.6	0.2	7.0
	May	1,075	4.0		4.6	0.4	8.9
	Jun	1,077	4.2		4.6	0.1	8.9
	Jul	1,439	3.1		3.5	0.0	6.7
	Aug	1,413	3.3		2.6	0.0	5.9
	Sep	1,667	2.5		2.9	0.0	5.3
	Oct	1,389	2.4		2.4	0.0	4.9
	Total	15,605	3.2		3.5	0.1	6.8
Central Arctic	Nov–Apr	5,746	0.9	1.4		9.3	11.6
	May	1,007	0.8	1.1		3.0	4.9
	Jun	1,056	0.8	0.8		1.7	3.2
	Jul	1,215	0.9	1.4		3.8	6.1
	Aug	1,017	1.2	2.1		3.5	6.8
	Sep	1,259	1.2	2.1		3.6	6.8
	Oct	980	1.2	1.6		6.4	9.3
	Total	12,280	1.0	1.5		6.3	8.7
Porcupine	Nov–Apr	4,463	0.0	0.0	0.9		0.9
	May	1,030	0.0	0.0	0.3		0.3
	Jun	812	0.0	0.0	0.7		0.7
	Jul	878	0.0	0.0	1.0		1.0
	Aug	699	0.0	0.0	0.9		0.9
	Sep	841	0.0	0.0	1.1		1.1
	Oct	689	0.0	0.0	1.2		1.2
	Total	9,412	0.0	0.0	0.9		0.9

for the TCH (Bonferroni adjusted pairwise comparisons; $\chi_1^2 = 11.3$, $P = 0.005$) and the CAH ($\chi_1^2 = 37.1$, $P < 0.001$) but not different from the PCH ($\chi_1^2 = 0.8$, $P = 1.000$). The PCH was also lower than the CAH ($\chi_1^2 = 12.8$, $P = 0.002$) but not different from the TCH ($\chi_1^2 = 3.0$, $P = 0.502$). The rate for the TCH was not different from the CAH ($\chi_1^2 = 5.5$, $P = 0.115$).

There were no differences among herds in the rate at which caribou that had moved to different herds returned to their initial herd ($\chi_3^2 = 2.9$, $P = 0.400$). There were apparent differences in the maximum length of time caribou spent with other herds; all animals initially with the WAH or PCH returned to their initial herd within 300 days after being designated with another herd, whereas 2 TCH and 1 CAH caribou remained with other herds for >2 years (Fig. 3).

When we looked at the early June calving period separately for comparison with previous studies, there were

Table 3. Percentage of all weekly female caribou locations determined to be in other herd ranges by year and initial herd and sample sizes, northern Alaska, USA, and Yukon Territories, Canada, 2003–2015.

	Western Arctic		Teshekpuk		Central Arctic		Porcupine	
Year	**%**	***n***	**%**	***n***	**%**	***n***	**%**	***n***
2003	0.0	1,118	8.7	635	1.2	1,091	0.0	427
2004	0.0	851	13.4	977	7.1	2,097	0.0	477
2005	2.1	473	10.6	1,009	4.4	1,678	0.0	605
2006	5.7	349	1.8	1,362	4.8	1,387	0.0	546
2007	0.0	676	0.9	1,517	0.0	284	0.0	667
2008	0.0	1,115	4.0	1,517	3.5	313	0.0	730
2009	0.6	1,238	5.3	1,478	2.5	717	0.0	688
2010	1.3	1,731	8.2	1,214	4.3	884	3.2	680
2011	0.9	2,644	7.8	1,119	12.5	769	0.2	619
2012	2.5	2,656	9.2	1,317	10.2	511	3.1	671
2013	1.2	2,802	9.4	1,275	4.1	634	1.7	1,034
2014	1.7	3,025	11.1	1,138	18.4	1,022	0.4	1,520
2015	2.8	2,633	2.4	1,047	37.5	893	1.7	748

Table 4. Number and percent of identified herd interchange events beginning in each month for female caribou, by initial herd, northern Alaska, USA and Yukon Territories, Canada, 2003–2015.

	Western Arctic		Teshekpuk		Central Arctic		Porcupine	
Month	Number	%	Number	%	Number	%	Number	%
Jan	0	0.0	3	10.0	4	10.5	1	16.7
Feb	0	0.0	0	0.0	7	18.4	0	0.0
Mar	0	0.0	0	0.0	0	0.0	1	16.7
Apr	0	0.0	3	10.0	0	0.0	0	0.0
May	0	0.0	5	16.7	1	2.6	1	16.7
Jun	0	0.0	4	13.3	0	0.0	1	16.7
Jul	0	0.0	1	3.3	10	26.3	2	33.3
Aug	0	0.0	3	10.0	1	2.6	0	0.0
Sep	2	18.2	3	10.0	1	2.6	0	0.0
Oct	4	36.4	2	6.7	10	26.3	0	0.0
Nov	4	36.4	5	16.7	1	2.6	0	0.0
Dec	1	9.1	1	3.3	3	7.9	0	0.0
Collar-yrs	603		441		338		260	

32 cases (individual caribou collared for 1 yr; $n = 1{,}218$) in which female caribou were assigned to other herds based on the MHI during the early June calving period. Based on the movement paths, 5 of these instances did not appear to be clear cases of being with the another herd during calving: 1 WAH female wintered with the TCH but returned to the WAH soon after the calving period; 2 TCH females wintered in western Alaska with the WAH, moved through the WAH calving grounds, did not calve, and then continued into the TCH range; 1 TCH female wintered with the CAH, was between herds during calving and then rejoined the TCH in late June; and 1 CAH female was with the PCH during winter and was not clearly with either herd during calving. After removing these 5 cases, there were 27 cases (2.2% of all cases) representing 20 different caribou in which an animal was with another herd during calving (Table 5). None of the 520 collar-years during calving from the WAH included a case of herd switching during calving; 0.5% of collar-years from the PCH, 7.4% of collar-years from the TCH, and 2.8% of collar-years from the CAH included cases of being with other herds during calving (Table 5).

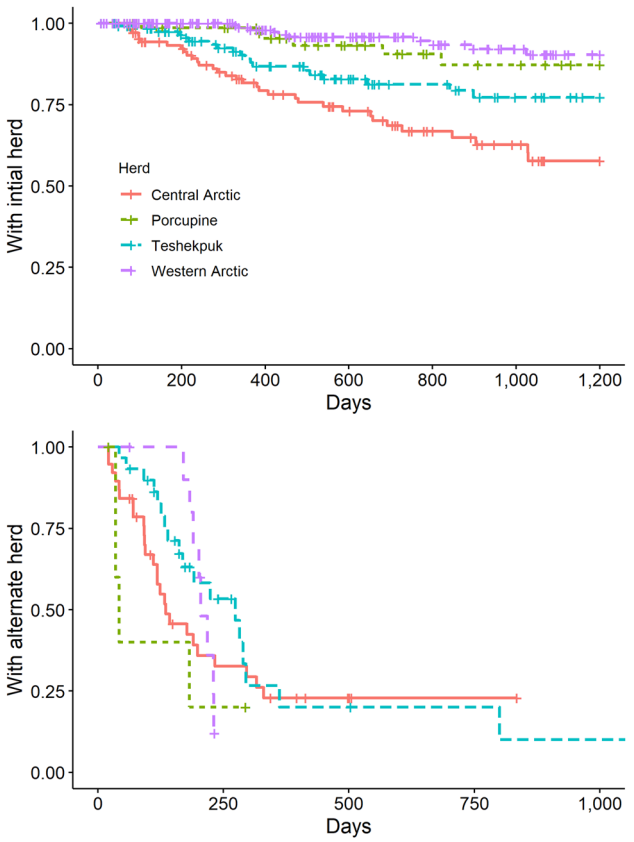

Figure 3. Kaplan-Meier test results of the proportion of female caribou remaining with the initial herd and proportion of animals remaining with another herd after a herd interchange event in northern Alaska, USA, or Yukon Territories, Canada, during 2003–2015.

Herd Overlap

The amount of herd overlap occurring in each of the herd's main ranges (defined by the weekly 75% isopleth) varied throughout the year (Fig. 4). The WAH had a very low amount of overlap with other herds throughout the year, although a small amount of herd overlap with the TCH did occur most of the year. The other 3 herds exhibited substantial overlap during the winter and the CAH and PCH also had substantial herd overlap during mid-summer when both herds may use the northeastern coast of Alaska. The TCH primarily overlapped with the WAH and CAH with up to 40% of CAH animals expected to be in the TCH range during winter (Fig. 4). Approximately 20% of PCH animals were expected to be in the CAH range during parts of a typical winter and a large proportion (>60%) of the CAH was expected to be in the PCH range during portions of a typical winter. Because the WAH and PCH are much larger than the CAH and TCH, approximately 50% of caribou within the CAH and TCH range (75% isopleth) during winter were expected to be from other herds (Fig. S4, available online in Supporting Information). Approximately 20% of caribou within the PCH range were expected to be from other herds during winter, but the proportion of caribou from other herds in the WAH range was expected to be low all year.

DISCUSSION

There was greater herd interchange from the 2 smaller herds to the 2 larger herds, indicating a tendency of caribou to join larger groups or move to areas of higher caribou density.

Table 5. Number and percentage of female caribou collar-years identified as being with other herds during the early June calving period, northern Alaska, USA, and Yukon Territories, Canada, 2003–2015.

		Herd during calving			
Measure	**Initial herd**	**Western Arctic**	**Teshekpuk**	**Central Arctic**	**Porcupine**
Number	Western Arctic	520	0	0	0
	Teshekpuk	9	237	10	0
	Central Arctic	2	2	243	3
	Porcupine	0	0	1	191
%	Western Arctic	100.0	0.0	0.0	0.0
	Teshekpuk	3.5	92.6	3.9	0.0
	Central Arctic	0.8	0.8	97.2	1.2
	Porcupine	0.0	0.0	0.5	99.5

There are many potential benefits for animals joining groups. Groups may form in response to high forage abundance, but they may also enable animals to better locate forage resources (Pöysä 1992) with less time devoted to vigilance behavior (Burger et al. 2000). A small proportion of informed individuals can help guide larger groups (Couzin et al. 2005); researchers have reported that animals can improve their ability to successfully complete long migratory movements by forming large groups and using collective navigation (Berdahl et al. 2016) and social learning from older animals (Mueller et al. 2013). Similarly, research on caribou has reported that larger groups of caribou may be more likely to detect predators while spending less time in vigilance behavior (Bøving and Post 1997) and individual risk of predation by wolves may decline at higher caribou densities (Dale et al. 1994). Torney et al. (2018) reported that migrating caribou copy directional choices of neighbors and Dalziel et al. (2016) reported that caribou exhibited more collective behavior during migration and shortly after calving but moved more independently during other times of the year.

Many species that aggregate in groups are managed based on administrative or geographic boundaries based on logistical considerations. Understanding how these groups extend across borders, cross borders during movements, or change in composition over time can aid management in these situations. Caribou in Alaska are managed by herd and interchange of individual caribou among herds was thought to have been relatively uncommon over the last several decades of caribou monitoring; however, data sets

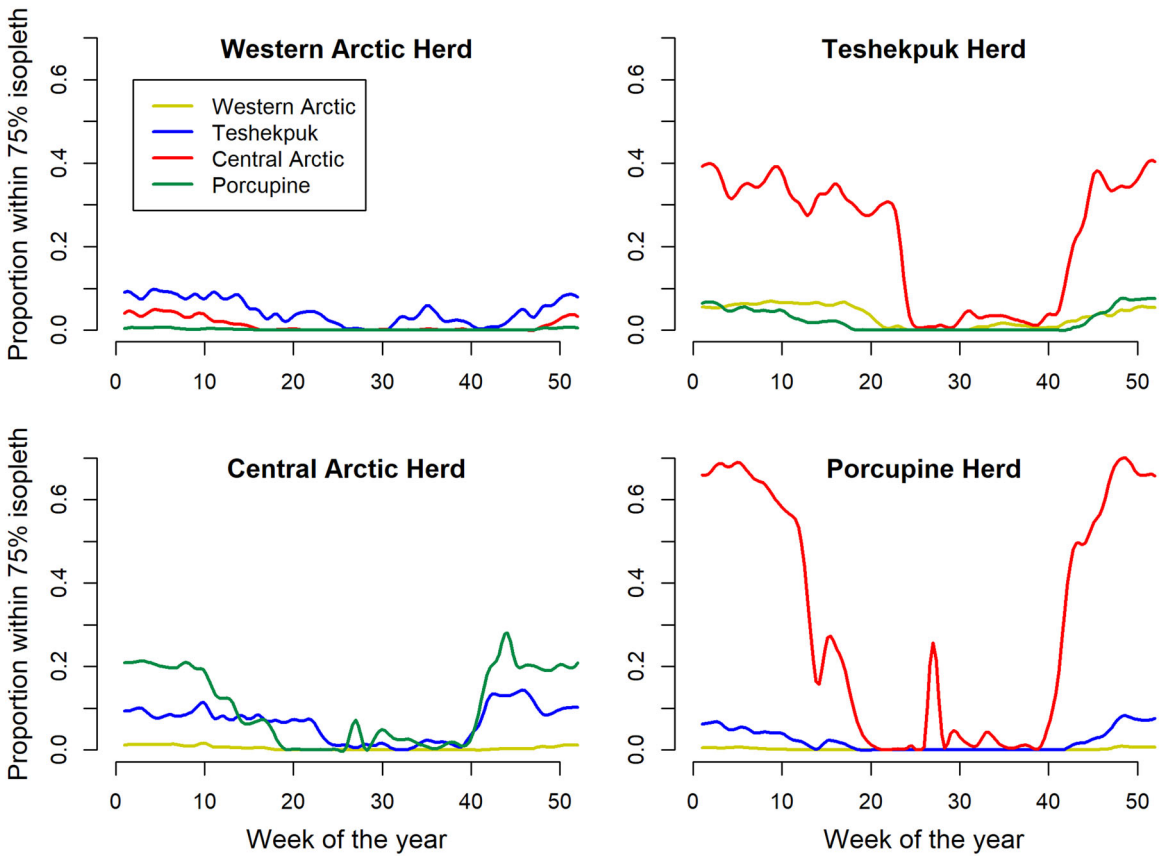

Figure 4. The proportion of female caribou from the other 3 herds predicted to be within a herd's 75% isopleth calculated by kernel density estimation by herd and week in northern Alaska, USA, or Yukon Territories, Canada, 2003–2015.

were generally small and there was a high degree of variability among results, with some larger movements reported (Boulet et al. 2007, Person et al. 2007). Based on our large data set derived from satellite-collars, larger herds (WAH and PCH) in our study tended to have less herd interchange than the smaller herds (TCH and CAH). Both smaller herds had relatively high proportions of collared caribou moving with other herds (Table 4; Fig. 3; Fig. S2) and movements from the 2 smaller herds were more frequent and had a longer maximum duration (Fig. 3).

The TCH and CAH were first recognized as separate herds in the 1970s (Davis and Valkenburg 1978, Lenart 2015, Parrett 2015) when telemetry data made it possible to track the movement of individual animals. Both herds have increased substantially in size since then, although both herds declined from their peak size during the study period. It is not clear if their higher rates of herd interchange are a result of their smaller herd size relative to neighboring herds, their location, or other demographic factors.

Being with other herds during calving, in early June, appeared to be very rare for females collared with the WAH or PCH, but we found that 7.4% of TCH cases were with another herd during calving (Table 5). This is similar to the 6.9% rate reported by Person et al. (2007) using some of the same data. Our rate of 2.8% for the CAH was also roughly similar to the 1.6% previously reported for the CAH based on very high frequency-collars (Cameron et al. 1986) at a time when the CAH was substantially smaller.

Because our dataset included only female caribou our results may not apply to males. Male caribou do not typically reach the calving area until after calving has occurred, if at all; therefore, they will not have high fidelity to calving areas. They also search out female caribou during the rut, which could result in increased movement among herds; both of these behaviors could contribute to increased likelihood of large changes in distribution. In the case of the TCH, there is a high degree of sexual segregation during the winter with many male caribou wintering in the Brooks Range, closer to other herds, and proportionally fewer males remaining on the Arctic Coastal Plain (Parrett 2015). Boulet et al. (2007) reported that microsatellite markers and space use data did not show sex differences in gene flow among caribou herds. Other genetic evidence suggested that male dispersal may be more frequent than female dispersal (McFarlane et al. 2016).

Cameron et al. (1986) studied female caribou in the CAH outfitted with very high frequency-collars and were only able to confirm 1 case out of 64 (1.6%) where a caribou emigrated to another herd and they did not observe any caribou collared with the PCH that were present on the CAH summer range. Roffler et al. (2012) reported that for females collared for ≥2 calving seasons, the percent of female caribou switching calving ranges between the Mentasta and Nelchina herds in central Alaska was 0.9% (1 of 108 collar-years; Mentasta to Nelchina) and zero (0 of 119 collar-years; Nelchina to Mentasta). These 2 herds had a high degree of overlap during the rut and were genetically similar based on nuclear DNA (Mager et al. 2014), but differences were evident with mitochondrial DNA (Roffler et al. 2012).

Bergerud (1996) suggested that large segments of caribou herds in Canada shifted among herds based on estimates of herd size and observations of large movements. Davis et al. (1986:107) reported that current concepts of calving grounds, herd fidelity, and dispersal needed to be revised "…to better explain dispersal to adjacent calving areas." But, Valkenburg et al. (2002:ii) concluded that although large herds may assimilate smaller herds, at that time there was "…no credible evidence that the interchange of groups of caribou between herds has ever occurred in Alaska." Similarly, Gunn and Miller (1986:151) reported that "… interchange between calving grounds has not yet been unequivocally documented." Later, Boulet et al. (2007) examined movements and genetic differentiation of 7 overlapping caribou herds in eastern Canada and reported that 9.4% of collared females (14 of 149) from 2 large migratory herds switched to the calving site of another herd at least once and large herd overlap occurred during the rut in some years. Hinkes et al. (2005) suggested that over long time periods, metapopulation theory may best describe caribou herd dynamics in southwest Alaska.

Herds experiencing herd growth may also expand their range, which could be expected to result in greater overlap and inter-herd movements. Skoog (1968) hypothesized that there were centers of habitation for caribou. These areas were used during periods of low population numbers, but when populations were high, caribou moved farther and movement patterns could become erratic. Although the available data to test this were imprecise, we found no clear link between herd growth rate and herd interchange in this study. The 4 herds exhibited markedly different population changes during this study: the WAH declined sharply, the PCH grew steadily, and the TCH and CAH increased in size and then declined in size. During this time, the CAH and PCH showed some increase in inter-herd movements, but the WAH and TCH did not. The relationships between annual herd size (interpolated between photo-censuses) and herd interchange rate were thus inconsistent. The correlation between annual herd interchange rate and interpolated herd size was negative ($r = -0.23$, $r = -0.38$, and $r = -0.61$) for the WAH, TCH, and CAH respectively, and positive ($r = 0.55$) for the PCH. The high correlation for the CAH was largely influenced by the high value in 2015 ($r = -0.30$ without 2015) when substantial overlap occurred during winter; the high correlation for the PCH was due to larger interchange rates in the last 6 years.

Defining herd interchange requires subjective definitions, but quantitative metrics of herd affinity may be useful for identifying periods of interchange that could influence vital rate estimation, harvest rates, or gene flow. Our MHI appeared to be generally successful at identifying inter-herd movements. The estimated rates of herd interchange depend on the cut points chosen, but because it provides a continuous metric between zero and 1, the cut point can be adjusted to use a higher or lower weight of evidence to assign herd changes. This metric does require a fairly large number of

active collars on all herds and it will work best when animals have distinctive seasonal herd ranges that are relatively consistently used during the study period. A limited number of collars for some herd and year combinations limited our analysis, particularly the use of the ACC component.

We developed our MHI for this specific situation with 4 herds with complex, irregular herd distributions with multiple wintering areas, varying levels of range overlap, and occasional unusual movements. In other studies, methods such as fuzzy c-means clustering have been successfully used to differentiate caribou herds based on spatial clusters (Schaefer et al. 2001, Nagy et al. 2011, Schaefer and Mahoney 2013) and can be used on Euclidean distances or on other metrics such as UDs calculated from KDE. We chose not to use fuzzy c-means clustering. Because of the complexity of our data, this method was not always able to ensure the delineated clusters corresponded to the 4 herds in our study, making this method infeasible for our purposes.

We tried to automate the process of identifying herd interchange to develop an objective metric for comparison among herds and time periods. For some purposes, adding an extra step of incorporating expert opinion to further screen the inter-herd movements identified through this automated process could be used to minimize errors in herd identity and to identify biologically meaningful herd changes or herd changes that are relevant to a specific management or research purpose.

Our herd overlap estimates indicate that, in a typical year, a large proportion of caribou in the winter range of the TCH and CAH are likely to be from other herds. These estimates are based on the combined kernels for 2003–2015, but in any single year the herds may only use a portion of their seasonal ranges; therefore, the herds could be more spatially segregated on an annual basis than suggested by this analysis. A large degree of herd overlap was apparent in collar locations during some winters, but it is difficult to enumerate how many caribou from other herds may be present in a given year based on collared animals alone.

Although the annual ranges of the TCH and WAH have a high degree of spatial overlap, the WAH has a low degree of overlap with other herds when calculated on a weekly basis. No caribou in WAH were identified in other herd ranges from July to August, a period when the WAH makes a very distinct, predictable movement across the Brooks Range (Dau 2015, Joly and Cameron 2017). The PCH also had strong herd cohesion with only 6 collared females out of 260 (Table 4) exhibiting evidence of herd interchange. The PCH has high annual range overlap with the CAH, yet few caribou from the PCH joined the smaller CAH. We restricted our analysis to these 4 herds, but the PCH also has some potential for interchange with other herds, especially the Fortymile Herd to the south. For example, in 1982, approximately 20,000 caribou from the PCH wintered with the Fortymile Herd south of the Yukon River (Valkenburg and Davis 1986), although whether any longer-term herd interchange occurred as a result is unknown.

Which factors lead to inter-herd movements is unknown, but our results, based on a limited sample of 4 herds, suggest that herd size and spatiotemporal overlap may play a role. It is not clear whether larger herds have inherently higher herd fidelity or if their larger size means they are less likely to encounter larger groups from other herds, but other studies have also documented animals from smaller herds joining larger herds. Semi-domestic reindeer in western Alaska have joined large groups of caribou in the WAH that move through the reindeer ranges (Finstad et al. 2002). Similarly, in 1994, approximately 35,000 caribou from the much larger (~170,000 caribou) Mulchatna Herd mixed with the smaller Kilbuck Herd (~4,000 caribou) in southwest Alaska and the majority of Kilbuck Herd animals adopted typical Mulchatna Herd movement patterns and 11 of 13 radio collared Kilbuck animals calved in the Mulchatna Herd's calving ground the following year (Hinkes et al. 2005).

The most direct potential effect of herd interchange is on herd size. The small Red Wine Mountains Herd of woodland caribou (*Rangifer tarandus caribou*) in eastern Canada declined in part because of emigration to the much larger George River Herd (Schaefer et al. 1999). In the second half of 2015, 6 of 18 collared caribou thought to have been initially with the CAH were determined to have joined the PCH after the 2 herds overlapped on the Arctic Coastal Plain in midsummer. Although this was near the end of our study period, which limited our inference, subsequent data suggested that a number of these caribou remained with the PCH. This movement was coincident with a sharp decline in the CAH herd size from an estimate of 68,000 in 2010 to just 23,000 in 2016. A large increase in adult female mortality was also noted during this time period, so how much of this decline was due to CAH animals joining the PCH remains unclear. The population size was not estimated each year during this period, making comparisons of population size and herd interchange more challenging.

Documenting the rate of inter-herd movements is important for management, but not all of the instances of herd interchange we identified may be meaningful, either biologically or for management purposes. In some cases, caribou use of adjacent herd ranges could just be considered atypical seasonal distributions occurring in areas used more reliably by other herds; however, this information may still be of interest to herd managers conducting surveys or assessing range quality. For instance, herd interchange occurring during the rut will have implications for gene flow among herds (Roffler et al. 2012), even if short-lived. Mixing at all times of year has potential implications for disease transmission, and when a large herd mixes with a small herd, less restrictive harvest regulations for a large herd can result in overharvest of the small herd (Pamperin 2015). If the manager knows herd mixing occurred during a photo-census, it can be partially accounted for by using statistical adjustments based on data from radio-collars of adjacent herds (Rivest et al. 1998, Lenart 2015).

MANAGEMENT IMPLICATIONS

Ungulate management is frequently conducted on the basis of individual herds that are treated as closed populations. Our results reveal that this assumption is not always correct.

Knowing when and to what extent herd interchange and overlap may be occurring can help herd managers more accurately estimate and track herd-specific demographic parameters such as population size, parturition rates, sex and age composition, and recruitment. These demographic parameters may then be used in population models to inform harvest regulations and make decisions related to permitting new development. We provide useful metrics for researchers and managers to quantify interchange rates. Smaller herds may act as source populations for larger herds given their higher rates and longer durations of inter-herd movements. Potential loss of individuals via herd interchange should be accounted for in the management of smaller herds.

ACKNOWLEDGMENTS

These data were provided by the ADFG, United States National Park Service, United States Fish and Wildlife Service, United States Bureau of Land Management, North Slope Borough, Government of the Yukon, Government of Canada, Government of the Northwest Territories, the Porcupine Herd Technical Committee, and ConocoPhillips Alaska. C. S. Swingley, D. Dissing, and P. Odom helped with data management, figures, and manuscript production. B. E. Lawhead, J. H. Welch, C. Krenz, B. B. Hansen, and anonymous reviewers provided helpful feedback on the manuscript. We also thank the many people who deployed or funded telemetry-collars used in the analysis, especially J. R. Dau, G. M. Carroll, D. A. Yokel, R. E. McGhee, and C. L. Rea. Funding for this analysis was provided by Shell Exploration and Production Company and the North Slope Borough. Special thanks to E. Westlien for initial funding and support of the analysis.

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Associate Editor: Steeve Côté.

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