**ARCTIC**
VOL. 68, NO. 4 (DECEMBER 2015) P. 407–421
http://dx.doi.org/10.14430/arctic4523

# What Happened to the Beverly Caribou Herd after 1994?

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(*Received 8 June 2014; accepted in revised form 27 April 2015*)

ABSTRACT. The Beverly herd was one of the first large migratory herds of barren-ground caribou (*Rangifer tarandus groenlandicus*) defined in northern Canada on the basis of annual return of breeding females to traditional calving grounds near Beverly Lake in Nunavut. In 1994, herd size was estimated at 276 000 ± 106 600 (SE) adult caribou, but monitoring was minimal from 1994 to 2007. The next calving ground survey in 2002 revealed that caribou densities had dropped by more than half since 1994; annual surveys following from 2007 to 2009 demonstrated an extreme decline in numbers of calving cows, and by 2011, no newborn calves were seen there. We examine two possible explanations for the declining use of the traditional Beverly calving grounds from 1994 until their abandonment by 2011. One explanation is that a true numerical decline in herd size occurred, driven in at least the later stages by low cow survival and poor calf productivity, which led the remaining Beverly cows to switch to the neighbouring Ahiak calving ground 250 km to the north in 2007–09 and join that herd. An alternative explanation is that the decline on the traditional Beverly calving grounds was largely due to a distributional shift to the north of the Beverly herd that may have begun in the mid-1990s. We suggest that the former explanation is the more likely and that the Beverly herd no longer exists as a distinct herd. We acknowledge that gaps in monitoring of Beverly and Ahiak caribou hamper definitive evaluation of the Beverly herd's fate. The large size sometimes achieved by barren-ground caribou herds is not a guarantee of persistence; monitoring shortfalls may hamper management actions to address declines.

Key words: Beverly; Ahiak; barren-ground caribou; decline; range shift; calving grounds; survival; productivity; monitoring

RÉSUMÉ. La harde de caribous de Beverly a été l'une des premières grandes hardes migratoires de caribous de la toundra (*Rangifer tarandus groenlandicus*) définies dans le nord du Canada en fonction du retour annuel des femelles reproductrices aux lieux de mise bas traditionnels situés près du lac Beverly, au Nunavut. En 1994, la taille de la harde était évaluée à 276 000 ± 106 600 (ES) caribous adultes, mais de 1994 à 2007, la surveillance a été minime. Le prochain recensement relatif aux mises bas a été réalisé en 2002, et celui-ci a révélé que les densités de caribous avaient chuté de plus de la moitié depuis 1994. De 2007 à 2009, des recensements annuels ont permis de constater le déclin prononcé du nombre de femelles en vêlage, si bien que vers 2011, on n'a aperçu aucun nouveau-né. Nous nous penchons sur deux possibilités pouvant expliquer le déclin de l'utilisation des lieux de mise bas traditionnels de Beverly de 1994 jusqu'à l'abandon de ces lieux vers 2011. Une explication veut qu'il y ait eu une chute réelle du nombre de membres de la harde attribuable, tout au moins vers la fin, au faible taux de survie des femelles et au faible taux de productivité des veaux, ce qui a mené le reste des femelles reproductrices de Beverly à opter pour le lieu de mise bas environnant d'Ahiak, à 250 km au nord entre 2007 et 2009, et à joindre cette harde. L'autre explication veut que le déclin enregistré aux lieux de mise bas traditionnels de Beverly soit grandement attribuable à la dérivation de la répartition vers le nord de la harde de Beverly, dérivation qui aurait pu commencer vers le milieu des années 1990. Nous suggérons que la première explication est plus plausible et que la harde de Beverly n'existe plus en tant que harde distincte. Nous reconnaissons que le manque de surveillance des caribous de Beverly et d'Ahiak a empêché de connaître de manière définitive le sort de la harde de Beverly. Parfois, la grande taille des hardes de caribous de la toundra n'est pas un gage de longévité. Les manques en matière de surveillance peuvent porter atteinte aux mesures de gestion à prendre pour contrer les déclins.

Mots clés : Beverly; Ahiak; caribou de la toundra; déclin; dérivation du parcours; lieux de mise bas; survie; productivité; surveillance

Traduit pour la revue *Arctic* par Nicole Giguère.

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## INTRODUCTION

One of the most conspicuous characteristics of barren-ground caribou (*Rangifer tarandus groenlandicus*) is that they return each year to traditional calving grounds (Kelsall, 1968; Skoog, 1968; Bergerud et al., 2008). Conventionally, the herds are named for their calving grounds (Skoog, 1968; Gunn and Miller, 1986). The Beverly herd was one of the first herds recognized in northern Canada from its traditional calving grounds near Beverly and Aberdeen Lakes and south of Garry Lakes (Kelsall, 1968). Mapping during 23 aerial surveys from 1957 to 1994 showed fidelity to these traditional calving grounds (Kelsall, 1968; Gunn and Sutherland, 1997; BQCMB, 1999a, b).

Herd size estimates for barren-ground caribou herds in the Northwest Territories and Nunavut generally are obtained as extrapolations from estimates of breeding cow numbers obtained during aerial photographic surveys at the peak of calving in June (Heard, 1985) or from post-calving surveys in July (Adamczewski et al., 2014). On the Beverly calving ground in 1994, the estimate was 120 000 ± 43 100 (SE) breeding cows with a density of 13.5 caribou 1+ year old/km$^2$, which was extrapolated to 276 000 ± 106 600 (SE) caribou 1+ year old in the herd (Williams, 1995). The trend in herd size from 1984 to 1994 was stable (Williams, 1995) and was similar to trends in most other Canadian migratory herds of barren-ground caribou at the time (Gunn et al., 2011). Caribou numbers in most herds were low in the 1970s, then increased until the mid-1990s to early 2000s, when they began to decline (Festa-Bianchet et al., 2011). Although the timing of peak abundance varies across North America, regionally the abundance of neighbouring herds is relatively synchronous (Gunn, 2003).

The Beverly herd has three immediate neighbouring herds with traditional calving grounds recorded through Aboriginal knowledge and aerial surveys: the Qamanirjuaq traditional calving grounds about 400 km to the southeast (Heard, 1983; BQCMB, 1999a, b), the Bathurst calving grounds about 450 km to the northwest (Heard, 1983; Gunn et al., 2012), and the Ahiak calving grounds 250 km north along the Queen Maud Gulf coast (Heard et al., 1987; Gunn et al., 2000, 2013a) (Fig. 1). Abundance increased to peak numbers in the 1980s and 1990s on all three calving grounds. The Qamanirjuaq herd increased from the 1970s and 1980s until 1994, when 496 000 (± 105 000 SE) caribou were estimated (Campbell et al., 2010). A survey in June 2008 estimated 349 000 (± 44 900 SE) caribou, which suggested a decline consistent with the declining trend in late winter calf:cow ratios, adult survival, and an increasing harvest rate (Campbell et al., 2010). The Bathurst herd peaked in the mid-1980s before declining 93% according to five calving ground surveys between 1986 and 2009 (Boulanger et al., 2011; Species at Risk Committee NWT, 2015). Low calf recruitment and a decline in the cow survival rate in 2000–06 contributed to the Bathurst decline (Boulanger et al., 2011). Trends for the Ahiak herd are more uncertain because of irregular survey frequency. Calving

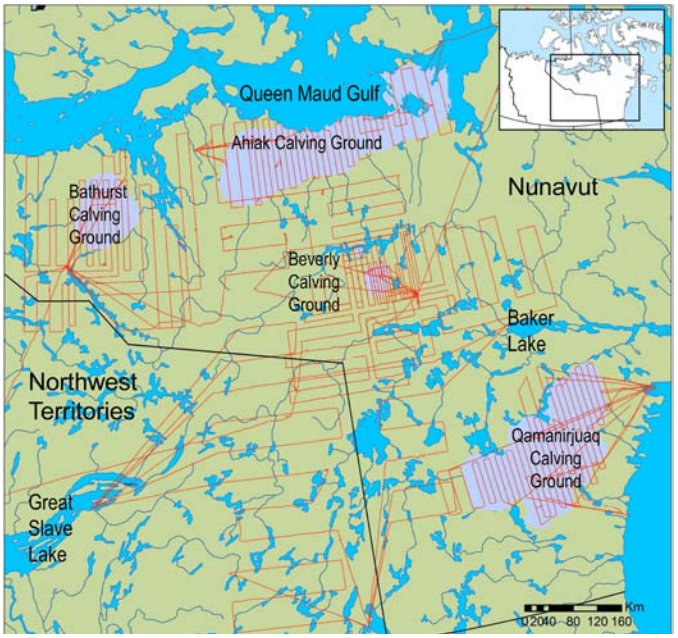


FIG. 1. Calving grounds of the Bathurst, Beverly, Ahiak, and Qamanirjuaq caribou herds in 2008, adapted from Poole et al., 2014. Survey lines (red) were flown in June 2008.

ground population or reconnaissance surveys (regularly spaced transects flown by small fixed-wing aircraft) took place in 1986, 1996, 2006–09, and 2011 (Gunn et al., 2000, 2013a; Adamczewski et al., 2009; Campbell et al., 2012; Poole et al., 2014). The 2011 survey (Campbell et al., 2012) had extended eastern boundaries; in this paper we use the Ahiak distribution as mapped by Gunn et al. (2013a) and Poole et al. (2014). Calving cow density on the Ahiak calving grounds increased between 1986 and 1996 and was similar in 1996 and 2006 (at 3.1 caribou/km$^2$), but it then declined rapidly from 2006 to 2009 (Adamczewski et al., 2009).

During 1994–2007, the period when neighbouring herds were declining, there was only a single aerial survey in 2002 to track abundance of the Beverly herd (Johnson and Mulders, 2009), and no vital rates (pregnancy rates, calf and adult survival) were monitored. The June 2002 aerial reconnaissance survey showed densities of 4.0 caribou 1+ year old/km$^2$, which was less than half the density in 1994 (Fig. 2; Johnson and Mulders, 2009). Subsequent aerial surveys in 2007–09 revealed progressively lower numbers of breeding cows on a reduced fraction of the traditional Beverly calving grounds (Fig. 2; D. Johnson, J. Williams and A. Kelly, unpubl. data 2007–09; Poole et al., 2014). By 2007, densities had fallen to 0.40 caribou 1+ year old/km$^2$ (Fig. 2; D. Johnson, unpubl. data 2007; Poole et al., 2014), a decline of 97% from 1994. Aerial coverage surrounding the 2007 and 2008 aerial reconnaissance of the traditional Beverly calving ground was extensive to reduce the likelihood of missing aggregations of calving caribou (Poole et al., 2014). By June 2009, a concentrated area of calving could no longer be defined on the traditional Beverly calving grounds (J. Williams, pers. comm. 2009) and no

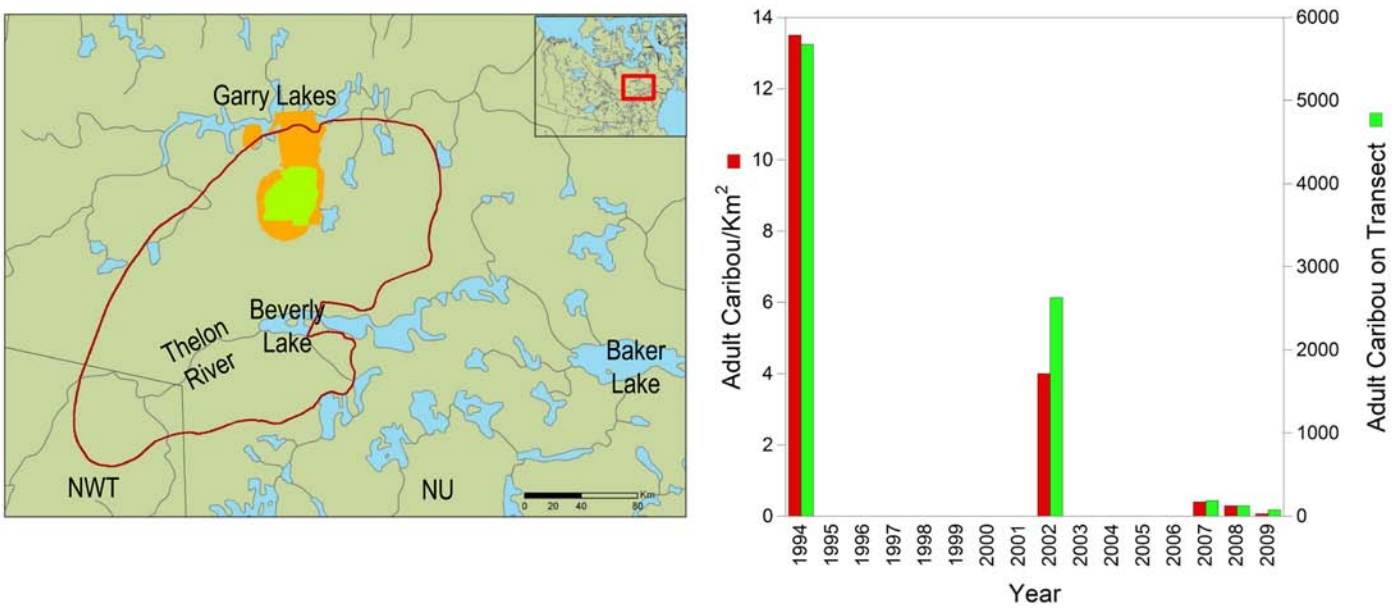


FIG. 2. (Left) Extent of calving on Beverly traditional calving ground in 2007 and 2008 (traditional calving ground defined by BQCMB, 2004; red outline); the green area was used in both years and the orange area in just one year. (Right) Decline in densities of caribou at least one year old seen on the Beverly calving ground (red) and number of adult caribou (green) recorded during reconnaissance surveys in 1994, 2002, 2007, 2008, and 2009.

calving caribou were seen there in June 2011 (Campbell et al., 2012).

Between 1994 and 2001, only two Beverly cows had been satellite-collared; these cows calved on the Beverly traditional calving ground (1995–97 and 2001–05; GNWT unpubl. data) and used the annual range defined by Heard (1983). Subsequently, in response to concerns over the low densities on the Beverly calving ground in 2002, 67 collars were fitted to adult cows on the Beverly and Ahiak caribou winter range, with herd affiliation assigned on the basis of calving grounds used in June (D. Johnson, unpubl. data 2006–08; Nagy et al., 2011). Eight cows that initially calved on the Beverly calving grounds switched in one of the following June periods to the coastal Ahiak calving grounds between 2006 and 2009 (this paper), while 13 were found only on the Beverly calving ground. This rate of switching was unusually high compared to the average annual emigration rate of 2%–5% detected between the Beverly and the neighboring Bathurst and Qamanirjuaq herds from eartag returns in the 1960s, 1970s, and 1980s (Parker, 1972; Heard, 1983).

The large decline in numbers of caribou on the traditional Beverly calving ground from 1994 to 2011 has two alternative explanations. Our purpose in this paper is to determine which of these two alternatives is best supported by the available evidence. One explanation is that there was a true numerical decline in Beverly herd size as death rates consistently exceeded birth and recruitment rates. The shift in calving distribution to the Ahiak herd's calving ground between 2006 and 2009 was a consequence of the collapse in calving densities as the remaining Beverly cows switched to maintain the advantages of gregarious calving (Gunn et al., 2012). If this explanation is correct, then the Beverly herd is no longer identifiable as a distinct herd. The alternative explanation is that range shift was the primary factor accounting for the decline on the traditional Beverly calving ground from 1994 to 2009: "However, by 2010, Beverly females had largely abandoned their ''traditional'' calving ground in favor of one used by the Queen Maude Gulf subpopulation. This shift in use likely began in the mid 1990s" (Nagy et al., 2011:2343). If this explanation is correct, then the Beverly herd has continued as a distinct subpopulation calving in Queen Maud Gulf, and was estimated at 124 200 ± 14 000 (SE) in 2011 (Campbell et al., 2012).

In our review of the evidence for these two explanations of the Beverly herd's fate, we acknowledge the uncertainty resulting from information gaps and limited sample numbers. To index demographic data for this paper, we used the pregnancy rates and adult cow survival measured through the satellite-collaring program from 2006 to 2009, as well as hunter kill data compiled by governments. We indexed productivity (birth rate and early calf survival) from observations of calf:cow ratios during aerial surveys at the peak of calving on the traditional Beverly calving grounds from 2007 to 2009. We compared these indicators to earlier demographic information from the Beverly herd and to the decline over the same period in the more closely monitored Bathurst herd. We also described the summer distribution and annual movements of Beverly and Ahiak satellite-collared cows. We used ground-based observations from the traditional Beverly summer range to determine whether Beverly summer distribution and relative abundance had changed from the mid-1980s to 2011. We then considered the implications of the uncertainty about what happened to the Beverly herd to conservation of barren-ground caribou.

## METHODS

### *Pregnancy Rates*

The pregnancy rates we used were assessed from progesterone levels in blood serum that we collected from cows captured on the winter ranges in March 2006 (n = 20) and April 2008 (n = 30) for satellite collaring (B. Elkin and D. Johnson, ENR unpubl. data). The 17 cows collared in 2007 were not used in this assessment because they were captured in July after calving had ceased.

### *Mortality and Switching of Calving Grounds*

We investigated the relative rates of "switching" of satellite-collared cow caribou between the Beverly and Ahiak calving grounds from 2006 to 2009. We measured individuals' rates of fidelity to each calving ground, and whether a cow's presence on either calving ground affected survival rates in the subsequent year. Herd identity of cows collared on the winter range was defined by their June locations in the year of capture or in subsequent years. We applied multi-strata models (Hestbeck et al., 1991; Brownie et al., 1993) to estimate rates of movement (also termed "transition probabilities") between calving grounds, yearly survival, and recapture rates using annual records of calving ground location. Recapture rate was the probability that a caribou that was collared and alive was observed in the following year. We categorized caribou as Beverly (B), Ahiak (A), or dead (D) between two calving seasons to accommodate the fact that most caribou died on ranges away from the calving grounds. In this context, the "dead" category estimates whether a caribou that was on the Beverly or the Ahiak calving grounds in the previous year was more likely to have died between calving ground seasons. Non-breeder cows were included in this analysis to increase sample sizes and reduce biased survival rate estimates. We added "non-breeder" as a sequential temporal covariate to assess whether breeding status affected transitions to the "dead" state or movement to other calving grounds.

The fit of multi-strata models was evaluated using the Akaike Information Criterion (AIC) index of model fit. The model with the lowest $AIC_c$ score was considered the most parsimonious, thus minimizing estimate bias and optimizing precision (Burnham and Anderson, 1998). The differences in $AIC_c$ values between the most supported model and other models ($\Delta AIC_c$) were also used to evaluate the fit of models when their $AIC_c$ scores were close. Any model with a $\Delta AIC_c$ score of less than 2 was worthy of consideration. Given the high mortality of Beverly collared caribou, we re-ran our analyses using the most supported initial model with mortalities censored from the data set to assess whether mortality rates created bias in movement rates.

### *Hunter Kill*

We used the annual levels of caribou harvested for the period 2004 to 2007 as compiled by the Beverly and Qamanirjuaq Caribou Management Board (BQCMB, 2005, 2006, 2007) from the territorial (Northwest Territories and Nunavut) and provincial (Manitoba and Saskatchewan) governments for the Beverly and Qamanirjuaq herds. These governments rely on conservation officer and hunter reports to summarize data from the caribou harvest, most of which occurs on the winter range.

### *Productivity*

During aerial reconnaissance surveys over the calving grounds in June of 2002 and 2007–09, the observers classified caribou as cows, calves, yearlings, or bulls on the basis of body size and whether antlers were light colored and polished or in velvet (Johnson and Mulders, 2009; Johnson et al., unpubl. data 2008, A. Kelly, unpubl. data). As an index to productivity, we calculated the maximum ratio of calves to cows during the sequential surveys and assumed that it represented productivity at the peak of calving.

### *Summer Distribution and Annual Movements*

Because spatial fidelity of migratory female caribou is highest during calving and summer (Schaefer et al., 2000), we mapped the accumulated collar data from Beverly and Ahiak caribou for June, July, and August before and after 2006. We also used the collar data to generate "average" seasonal collar pathways by smoothing the individual caribou pathways into splines, following the methods of Gunn et al. (2013b). We included the 1996–98 and 2001–05 Beverly and Ahiak collars for comparison with collared cow locations from 2006 to 2009. Collared cows were considered Beverly, Ahiak, or "Switched" on the basis of their locations in June. The term "switched" refers to collared caribou that were on the traditional Beverly calving grounds at least once in June and then were found on the Ahiak calving grounds at least once in a subsequent June.

One author (A. Hall) is a wilderness canoeing guide and biologist who kept a detailed journal about numbers and distribution of caribou from the same river routes in the traditional Beverly summer range each year from 1971 to 2014. We mapped his annual observations of caribou from 1984 to 2011 and assessed changes in relative numbers and distribution of caribou seen during his annual trips.

## RESULTS

### *Pregnancy Rates*

Five of seven (71%) Beverly cows (animals that calved on the Beverly traditional calving grounds) captured in March 2006 were pregnant. In April 2008, 13 of 29 (45%) Beverly

TABLE 1. $AIC_c$ model selection[1] for multi-strata analysis of calving ground exchange for collared cows from the Beverly and Ahiak caribou herds, 2006–09.

| Survival | | Movement | | Model selection | | | | |
|---|---|---|---|---|---|---|---|---|
| Beverly | Ahiak | Beverly-Ahiak | Ahiak-Beverly | $AIC_c$ | $\Delta AIC_c$ | $w_i$ | K | Deviance |
| constant | constant | constant | constant | 165.94 | 0.00 | 0.293 | 5 | 155.3 |
| constant | constant | breeder | constant | 167.62 | 1.68 | 0.127 | 6 | 154.6 |
| trend | constant | constant | constant | 167.81 | 1.87 | 0.115 | 6 | 154.8 |
| breeder | constant | constant | constant | 168.13 | 2.19 | 0.098 | 6 | 155.2 |
| constant | breeder | constant | constant | 168.21 | 2.27 | 0.094 | 6 | 155.2 |
| trend | constant | trend | constant | 168.25 | 2.31 | 0.092 | 7 | 152.9 |
| constant | constant | trend | constant | 169.02 | 3.08 | 0.063 | 6 | 156.0 |
| year | constant | year | constant | 169.43 | 3.48 | 0.051 | 9 | 149.3 |
| constant | Trend | constant | trend | 170.16 | 4.22 | 0.036 | 7 | 154.8 |
| breeder | breeder | trend | constant | 170.45 | 4.51 | 0.031 | 7 | 155.1 |
| year | year | year | year | 182.18 | 16.23 | 0.000 | 13 | 151.6 |
| trend | trend | trend | trend | 184.31 | 18.37 | 0.000 | 9 | 164.1 |

[1] Akaike Information Criteria ($AIC_c$), the difference in $AIC_c$ values between the *i*th and most supported model ($\Delta AIC_c$), Akaike weights ($w_i$), number of parameters (K), and sum of penalties are presented. 'Constant' means that the parameter did not vary for any of the years of the analysis, 'trend' means that a linear trend was assumed, 'breeder' means that breeding status (breeder vs non-breeder) affected the parameter, and 'year' means that the parameter varied from year to year.

and Ahiak cows captured were pregnant (D. Johnson and B. Elkin, ENR, unpubl. data.).

*Mortality and Switching of Calving Grounds*

In the multi-strata modeling, since the fate or use of a calving ground by collared individuals was usually determined, the recapture rate (which was set to be constant for all strata) was estimated at 0.95 (SE = 0.023, CI = 0.88–0.98). Six of 17 Beverly cows collared in July 2007 died within four to six weeks of capture and were not used in this analysis, as these early mortalities could have been capture-related. Other caribou mortalities following the July 2007 collar deployment occurred 6.1, 8.1, 13.4, 19.0, 21.9, and 23.1 months after collaring and were included in the analysis. The resulting data set had 55 individual caribou and 136 calving locations that indicated calving ground membership of individual caribou in successive years (Table 1). Of the 55 caribou, 13 occurred only on the Beverly calving grounds, 34 were only on the Ahiak calving grounds, and eight were on both calving grounds at least once. One cow had a four-year June calving ground sequence of Beverly/Ahiak/Beverly/Ahiak.

Model selection for the multi-strata model did not detect temporal trends in exchange rates between calving grounds or in mortality, but did reveal asymmetry in the exchanges (Table 2, Fig. 3). The probability of cows switching from the Ahiak to the Beverly calving grounds was 0.02, and the probability of Ahiak cows returning to the Ahiak calving grounds was 0.78 (Fig. 3). Conversely, the probability of cows returning to the Beverly calving grounds (0.28) was similar to the probability they would switch to the Ahiak calving grounds (0.31). Annual mortality of Ahiak collared cows averaged 0.21, while mortality of Beverly collared cows averaged 0.40 (Fig. 3 top panel).

Caribou that were on the Beverly calving grounds were more likely to die before the next calving season than caribou that moved to the Ahiak calving grounds. We note that higher mortality of Beverly cows resulted in a data set dominated by cows with a higher likelihood of moving to the Ahiak, potentially biasing estimates of movement rate. To explore this bias, we re-ran the most supported model in Table 1, but with the "dead state" removed. We also removed from the analysis any collared cows that had died after being on the Beverly or Ahiak calving ground in June but before the next calving season. Estimates of movement from Beverly to Ahiak increased to 0.53 (CI = 0.29–0.76) from 0.31 (CI = 0.16–0.51) (Table 2), whereas estimates of movement from Ahiak to Beverly were unchanged at 0.02 (CI = 0.003–0.14).

*Hunter Kill*

The Beverly and Qamanirjuaq Caribou Management Board (BQCMB) compiled caribou harvest levels from the two territories and two provinces primarily from estimates made by wildlife officers in the four jurisdictions. After 2008–09, the BQCMB was no longer able to report harvests because information was not received reliably from government agencies and there were difficulties in assigning harvests to subpopulations when the Beverly, Ahiak, and Qamanirjuaq herds overlapped in winter distribution. In the winters of 2004–05, 2005–06, and 2006–07, the estimated harvest from the Beverly herd was relatively constant at ~4050 caribou, mostly cows (BQCMB, 2005, 2006, 2007). Traditionally, hunters from northern Saskatchewan and southern Northwest Territories had been the main harvesters of the Beverly herd on the winter range (Gordon 1977, 1996, 2005). This harvest likely included caribou from adjacent herds in some winters, given overlap and annual variability of winter ranges.

TABLE 2. Model averaged multi-strata estimates (*p*), standard errors (SE), confidence limits (CI), and sample sizes (*n*) for analysis of Beverly-Ahiak calving ground exchange 2006–09.

| | Previous stratum[1] | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ahiak | | | | Beverly | | | | Other collar events | | |
| Current stratum[1] | *n* | *p* | SE | CI | *n* | *p* | SE | CI | First year | One year | Total |
| Ahiak | *44* | *0.78* | *0.05* | *0.65–0.86* | 8 | 0.31 | 0.09 | 0.16-0.51 | 35 | 0 | 87 |
| Beverly | 1 | 0.02 | 0.02 | 0.00–0.11 | *7* | *0.28* | *0.09* | *0.13–0.47* | 19 | 1 | 27 |
| Dead | 12 | 0.21 | 0.05 | 0.12–0.33 | 9 | 0.40 | 0.11 | 0.22–0.62 | 0 | 0 | 21 |
| Total | 57 | 1.00 | | | 24 | 1.00 | | | 54 | 1 | 135 |

[1] Current and previous strata refer to the sequential ordering of movements between strata. Other collar events pertain to caribou that were in the database but did not directly contribute to the analysis since data were available for only one year. Cells with estimates of fidelity are in italics.

*Productivity*

Productivity, as indexed by calf:cow ratios at the peak of calving on the traditional Beverly calving ground in June, was 32:100 in 2007, 15:100 in 2008, and 2:100 in 2009 (D. Johnson, J. Williams and A. Kelly, unpubl. data 2007–09).

*Summer Distribution and Annual Movements*

The two collared Beverly cows (one in 1995–97 and one in 2001–05) consistently used the traditional Beverly calving and summer ranges south of Garry Lakes identified by Heard (1983), while the 30 Ahiak cows collared between 1996 and 2005 were nearly all farther north between the coast of Queen Maud Gulf and Garry Lakes (Fig. 4), with a few locations southwest and south of Bathurst Inlet. The six cows collared in March 2006 and found on the inland Beverly calving ground in June that year spent the summer south of Garry Lakes and within the traditional Beverly summer range (Fig. 4). The 15 cows collared in March 2006 and found on the Ahiak calving ground in June that year spent the summer north of Garry Lakes as far as the Queen Maud Gulf coast. From 2007 to 2009, locations of Beverly, Ahiak, and Switched collars increasingly overlapped on the Ahiak range, and the calving and summer ranges of Beverly and Ahiak caribou were no longer distinct.

Prior to 2006, the overall annual movements of the two Beverly and 30 Ahiak collared caribou showed distinct patterns, with little overlap during any season (Fig. 5). In 2006, Beverly and Ahiak collared cow movements were still relatively distinct, but from 2007 to 2009 Beverly, Ahiak, and Switched collared cows showed increasingly convergent movements.

All of the river sections traveled by A. Hall at least once from 1984 to 2011 (Fig. 4) overlap areas used by the two earlier Beverly collared cows in the Thelon watershed during summer in 1995–97 and 2001–05. Hall's river trips in the traditional Beverly summer range from 1984 to 2011 included an extended section of the lower Thelon River ending at Beverly Lake in 22 of those 28 years (Fig. 6). River trips also frequently included the upper Thelon River and the Elk River, which flows into the Thelon. The number of days on the Thelon River and other regional rivers varied annually, averaging 68.4 days per year, and declined slightly over time (Fig. 7a). From 1984 to 1996, caribou were seen an average of 19 days per year with no clear trend; however, after 1996 sightings declined, reaching a low of two days per year in the late 2000s. The average number of caribou seen per day was highly variable, but dropped by an order of magnitude between 2003 and 2007 (Fig. 7b). From 2006 to 2011, the total number of caribou seen each year averaged 11.

Hall, who first began observing Beverly caribou in 1971, noted an overall decline in relative numbers of calves on the Beverly summer range after 1997. He was used to seeing variable numbers of calves at heel with their mothers, and did not normally record calf:cow ratios. It was in three years (1998, 2001, and 2003) when he saw exceptionally low calf:cow ratios that he recorded the following observations. On 14 July 1998, Hall observed a group of 2000–3000 caribou 30 km from the junction of the Hanbury and Thelon Rivers and wrote: "99% barren cows—some yearlings and bulls. We saw only four calves—at least I hope they were barren cows and hadn't lost their calves or else it was a disastrous calving season." In the summer of 2001 on the Baillie River 10 miles from the junction with the Back River, Hall observed: "20 000–30 000 caribou seen on Baillie River on July 16; mostly cows but only one calf per 30–50 cows." In the summer of 2003, from a site near the junction of the Mary Frances River with the Thelon, Hall recorded: "5000 or more caribou seen on upper Thelon River on August 2; about 90% cows but virtually no calves - estimated only 1–2% calves." Hall noted that since 2009–10, even at traditional Thelon River crossings with records of Aboriginal hunting dating back thousands of years (Williams and Gunn, 1982; Gordon, 1996), he had been unable to find any recent caribou tracks in the river-bank sand.

## DISCUSSION

The trend toward reduction then disappearance of calving caribou on the traditional Beverly calving grounds is clear from the aerial surveys conducted during 1994, 2002,

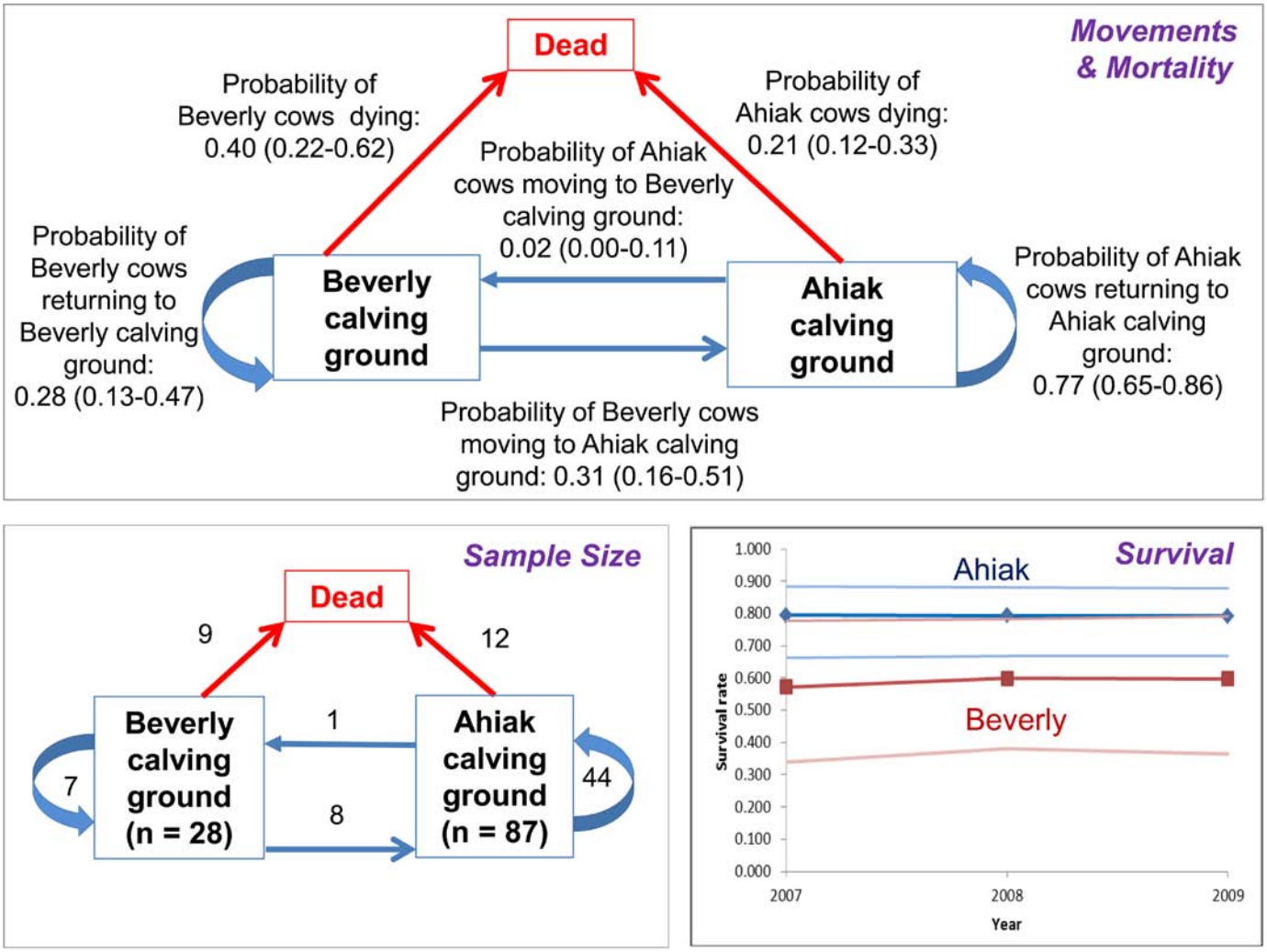


FIG. 3. Multi-state analysis of radio-collared Beverly and Ahiak caribou in 2007–09, showing model-averaged movements between calving grounds and mortality of caribou (top panel), sample size (bottom left), and trends in survival with variance (bottom right). Red arrows show probabilities of mortality and blue arrows show probabilities of switching or returning to the same calving ground.

and 2007–11 (Williams, 1995; Johnson and Mulders, 2009; Campbell et al., 2012; Poole et al., 2014). There is also limited evidence from collared caribou for some shift in calving ranges from the Beverly to the Ahiak calving grounds between 2006 and 2009. However, monitoring gaps and limited sample sizes, especially between 1994 and 2006, add uncertainty to any explanation for these trends. In the discussion below, we re-visit the evidence that supports the alternative explanations of decline, range shift, or both in the Beverly herd after 1994.

The evidence for the earlier stages of the decline (1994–2006) is meagre; it includes the reduced density of caribou on the traditional Beverly calving ground in 2002 and the three years after 1997 when there was evidence of exceptionally low calf:cow ratios. While there are only limited data on harvesting, there were concerns about harvesting by 2001. During the November 2001 BQCMB meeting, community board members from northern Saskatchewan were concerned about the status of the Beverly herd because the caribou harvest had increased as the herd became more accessible to southern Saskatchewan residents (Johnson and Mulders, 2009).

There is more evidence for a steep Beverly decline occurring between 2006 and 2011, as the vital rates were low during that time. The pregnancy rate for 29 Beverly and Ahiak cows in April 2008 was 45%, low compared to 76%–100% rates measured from a large series of known-age Beverly cows collected between 1979 and 1987 (Thomas and Barry, 1990a). The March 2006 pregnancy rate (71%) was also slightly lower than the long-term average, but was based on only seven cows. The low pregnancy rate in 2008, though based on a limited sample, is consistent with a later peak in calving, which suggests that cows were in below-average condition prior to the rut and during the winter (see Crête et al., 1993). The peak of calving on the traditional Beverly calving grounds shifted from 4–9 June in 1988, 1994, and 2002 (Gunn and Sutherland, 1997; Johnson and Mulders, 2009) to 12–15 June in 2007, 2008, and 2009 (D. Johnson, J. Williams and A. Kelly, unpubl. data 2007–09).

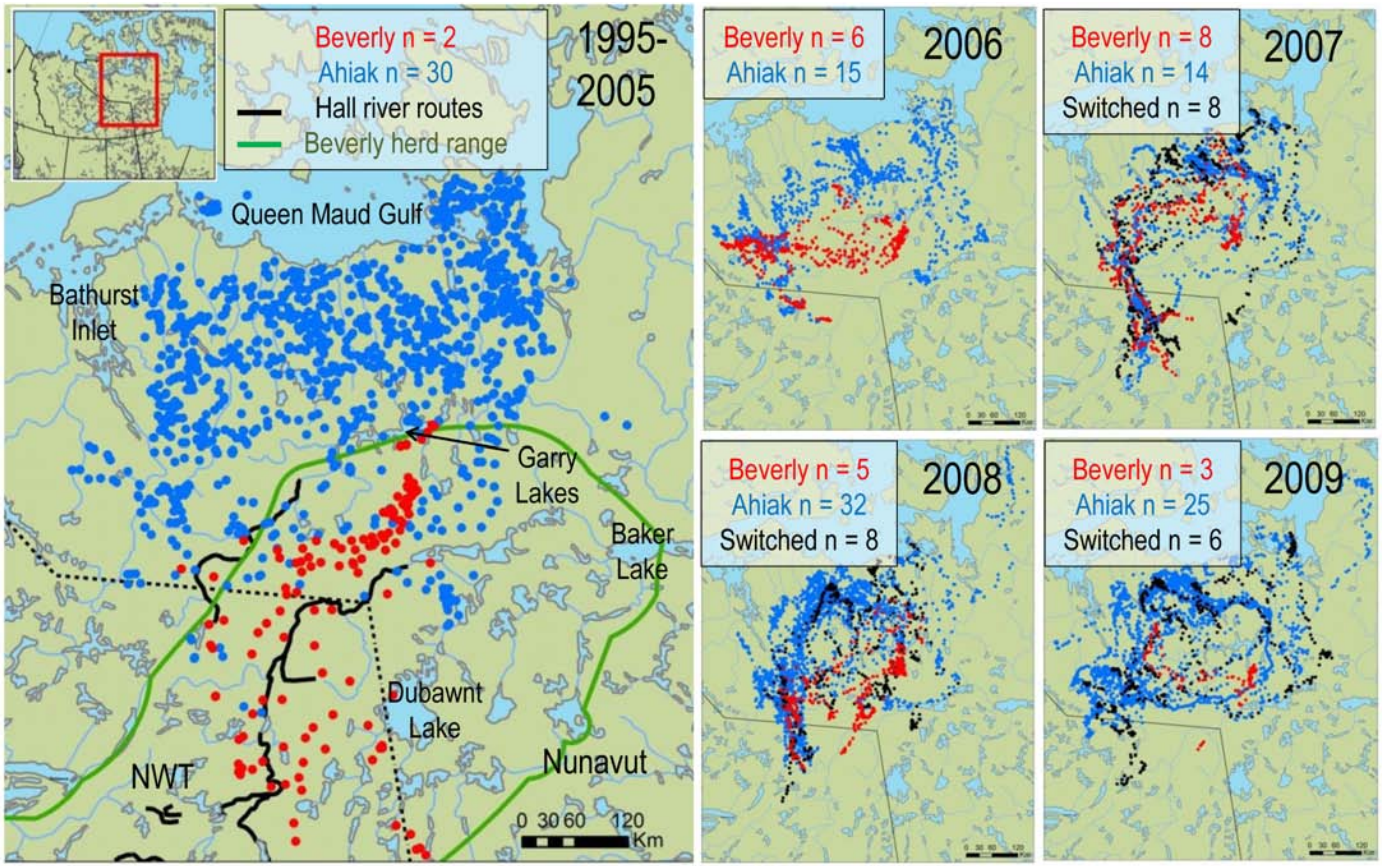


FIG. 4. Calving and summer (June–August) locations of satellite radio-collared Beverly and Ahiak caribou before and after 2006. 'Switched' refers to caribou that calved on the traditional Beverly calving grounds at least once but moved to the Ahiak calving grounds in subsequent years, regardless of whether they returned. Black lines show river sections traveled by A. Hall during his annual river trips from 1984 to 2011. The Beverly herd range (green outline) is adapted from Heard (1983).

The mean Beverly calf:cow ratio in June 2007, 2008, and 2009 was 16.3 ± 8.7 (SE), which suggests exceptionally low pregnancy rates, low early calf survival, or both. This low productivity contrasts with ratios of 60–80 calves per 100 cows observed just after the peak of Beverly calving during the 1980s and 1990s (Gunn and Sutherland, 1997). In June 2002, Johnson and Mulders (2009) recorded 53–75 calves per 100 cows.

The 40% annual mortality of collared cows that had calved on the traditional Beverly calving grounds was twice as high as that of Ahiak cows for 2006–09. The survival rates estimated in 2006–09 are based on a limited sample, and the age structure of the collared cows was unknown, so the results should be viewed with caution. Previously, age-specific Beverly survival rates for females more than three years old were estimated as 83% from life table analysis (Thomas and Barry, 1990b) when the herd was considered stable. Similarly, adult cow survival rates exceeding 80% were required for stability in the Bathurst (Boulanger et al., 2011) and George River herds (Crête et al., 1996).

Between 2007 and 2009, fidelity to the Beverly calving grounds was low (28%) and the probability of Beverly cows' switching to the Ahiak calving grounds was relatively high (31%). On the basis of hunter returns of ear-tags placed on Beverly and Qamanirjuaq caribou in the 1960s and 1970s, Parker (1972) noted that 6.1% of the Qamanirjuaq ear-tags were found in the normal range of the Beverly population and 4.5% of the Beverly ear-tags were found in the normal range of the Qamanirjuaq herd. Using a more extensive ear-tag data set, Heard (1983) estimated mean annual dispersal rates of 1.8% from the Beverly herd and 2.4% from the Qamanirjuaq herd. These results suggest a high Beverly range fidelity in these decades. Sample sizes were relatively low, but switching from the Beverly to the Ahiak calving grounds in 2006–09 appeared to increase the probability of survival for the cows. The sample of two satellite-collared cows monitored in 1995–97 and 2001–05 is too small to estimate fidelity over these years; however, we note that their summer and annual range-use patterns are consistent with the annual range for this herd defined in the 1970s and 1980s by Heard (1983).

In 2006, six collared Beverly cows largely maintained fidelity to the Beverly summer range; the movements for pre-calving to fall overlapped the movements of the two earlier Beverly collared caribou (1995–97 and 2001–05) and were within the annual Beverly range defined by Heard (1983). Seasonal fidelity is highest for calving and summer ranges in migratory barren-ground caribou (Cameron et al., 1986; Gunn and Miller, 1986; Schaefer et al., 2000; Nagy et al., 2011). The average movements (spline analysis) also

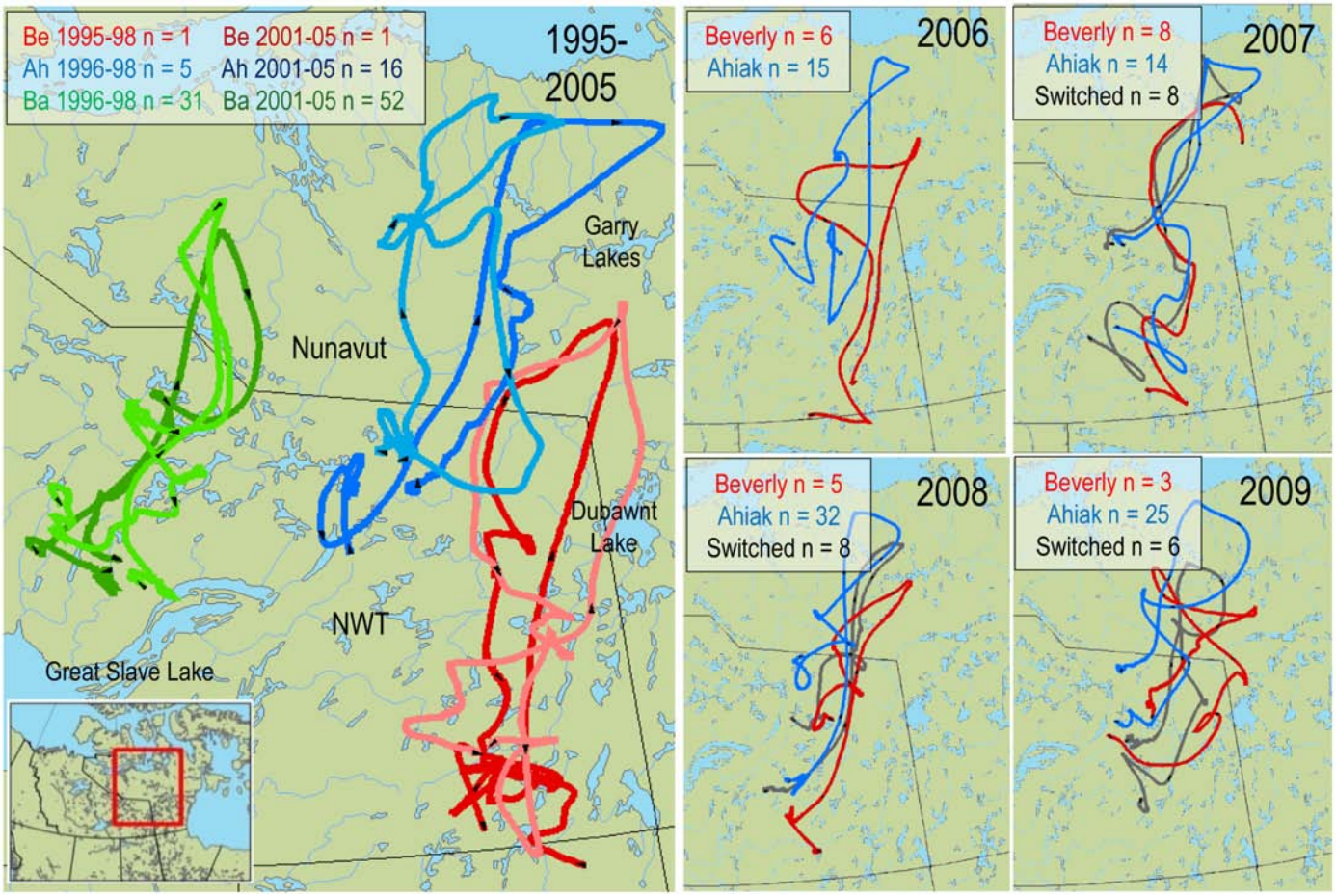


FIG. 5. Averaged seasonal movements (splines) of radio-collared Beverly and Ahiak collared caribou before and after 2006. Splines for Bathurst (Ba) collared caribou 1996–98 and 2001–05 (adapted from Gunn et al., 2013b) are included for comparison with the earlier Beverly (Be) and Ahiak (Ah) collars.

suggest that until 2006, the Beverly and Ahiak movement patterns had little spatial overlap (Fig. 5).

The declines in caribou group sizes and overall numbers seen by A. Hall in summers became strongly evident after 2004, suggesting reduced use of the traditional Beverly summer range by caribou. On their own, the reduced numbers of caribou seen by Hall could be evidence of either range shift or decline, but the timing of the reduction in use does not support the explanation of a shift beginning in the mid-1990s.

The demography of the Beverly herd from 2006 to 2011 can be compared to the Bathurst herd's decline, for which more data were available. Estimated adult female annual survival of Bathurst cows declined from 86% in 1985 to 67% in 2009 (Boulanger et al., 2011), compared to 60% in Beverly cows during 2006–09. The calf:cow ratios on the Bathurst herd's calving grounds from 1986 to 2012 averaged 65.7 ± 3.8 (SE), much higher than the ratios on the Beverly traditional calving grounds in 2007, 2008, and 2009 (2–32 calves:100 cows). Demographic modeling of the Bathurst herd decline showed that low recruitment and low adult survival could alone account for that herd's annual rates of change of up to −23% during 2006–09, with no evidence of significant emigration (Boulanger et al., 2011). The accelerating effects of a substantial harvest in naturally declining herds were demonstrated concurrently (from 2000 to 2006–09) in the Bathurst (Boulanger et al., 2011), Cape Bathurst, and Bluenose-West herds (Adamczewski et al., 2009) and may have contributed to a decline in the Beverly herd. However, the evidence for collar movement between the Beverly and Ahiak calving distributions between 2006 and 2009 indicates that decline alone does not account for the disappearance of calving caribou from the inland Beverly calving ground by 2011.

While the evidence is clear that between 2006 and 2009 there was only a 28% fidelity of Beverly cows to their traditional calving ground and a 31% probability that collared Beverly cows switched to calving on the Ahiak herd's calving grounds, we found no evidence for a shift of Beverly caribou to the Ahiak range prior to 2007. The 2006 calving locations of the six satellite-collared Beverly cows were within the traditional calving grounds, and their placement was similar to the mapped distribution in 2002 and all but two years from 1978 to 1994 (Gunn and Sutherland, 1997). For the other two years (1984 and 1987), the extension of calving was within 10–20 km of the delineated traditional calving ground (Gunn et al., 2007; Johnson and Mulders, 2009).

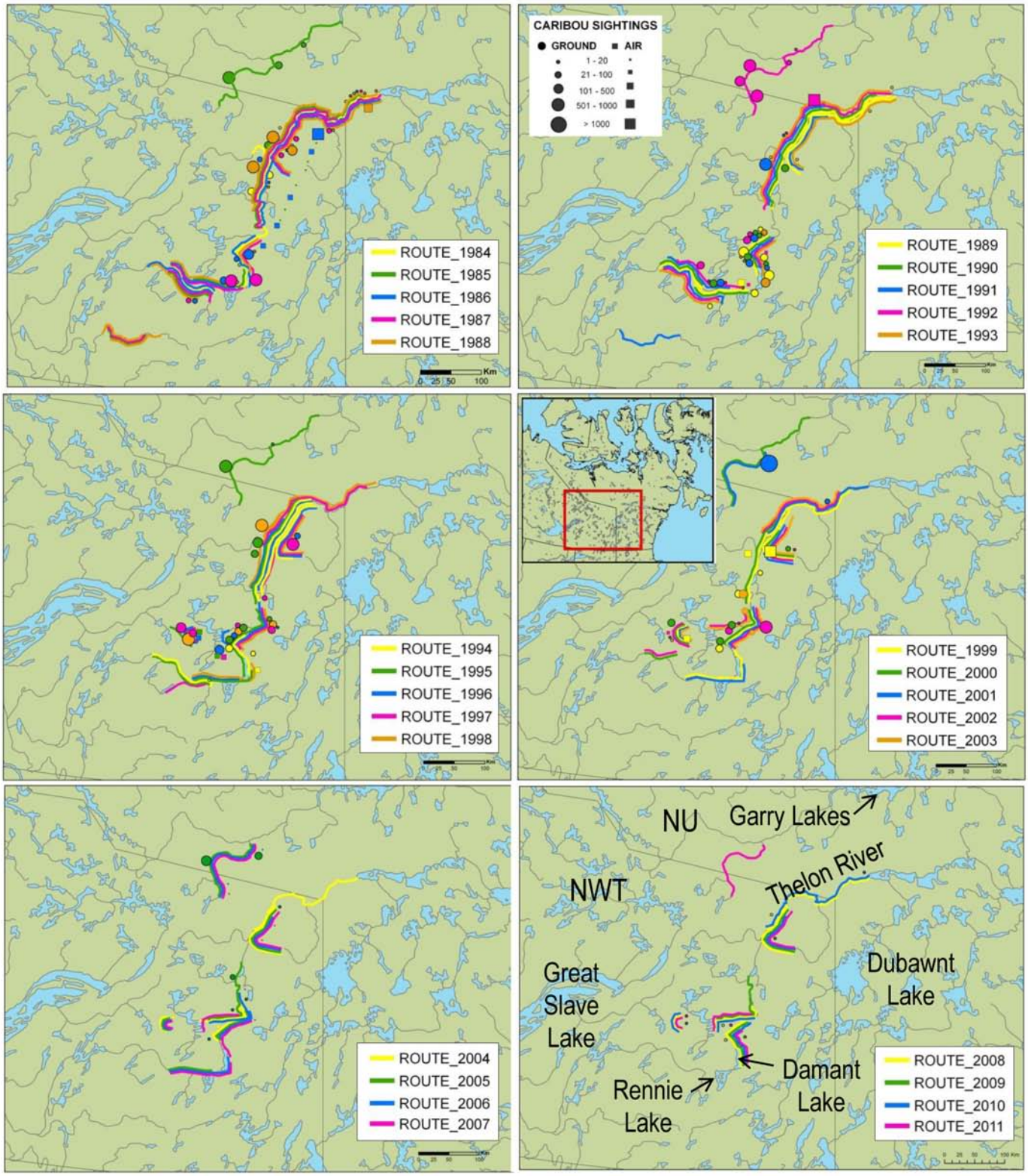


FIG. 6. River routes and caribou observations by Alex Hall in periods of four or five years during 1984–2011. Coloured lines show each year's river trips, and circles of the same colour show the sizes of the caribou groups seen on each trip. Coloured squares show caribou groups seen from the air.

Rates of exchange between the Beverly and neighbouring herds were estimated earlier at 1.9%–2.4% (Heard, 1983), a rate similar to average exchange rates of 3% for the Bathurst herd with the Ahiak and Bluenose-East herds in 1996–2009 estimated from satellite-collared cow locations (Adamczewski et al., 2009) and average exchange rates of 3.6% among satellite-collared cows from the Tuktoyaktuk Peninsula, Cape Bathurst, Bluenose-West, and

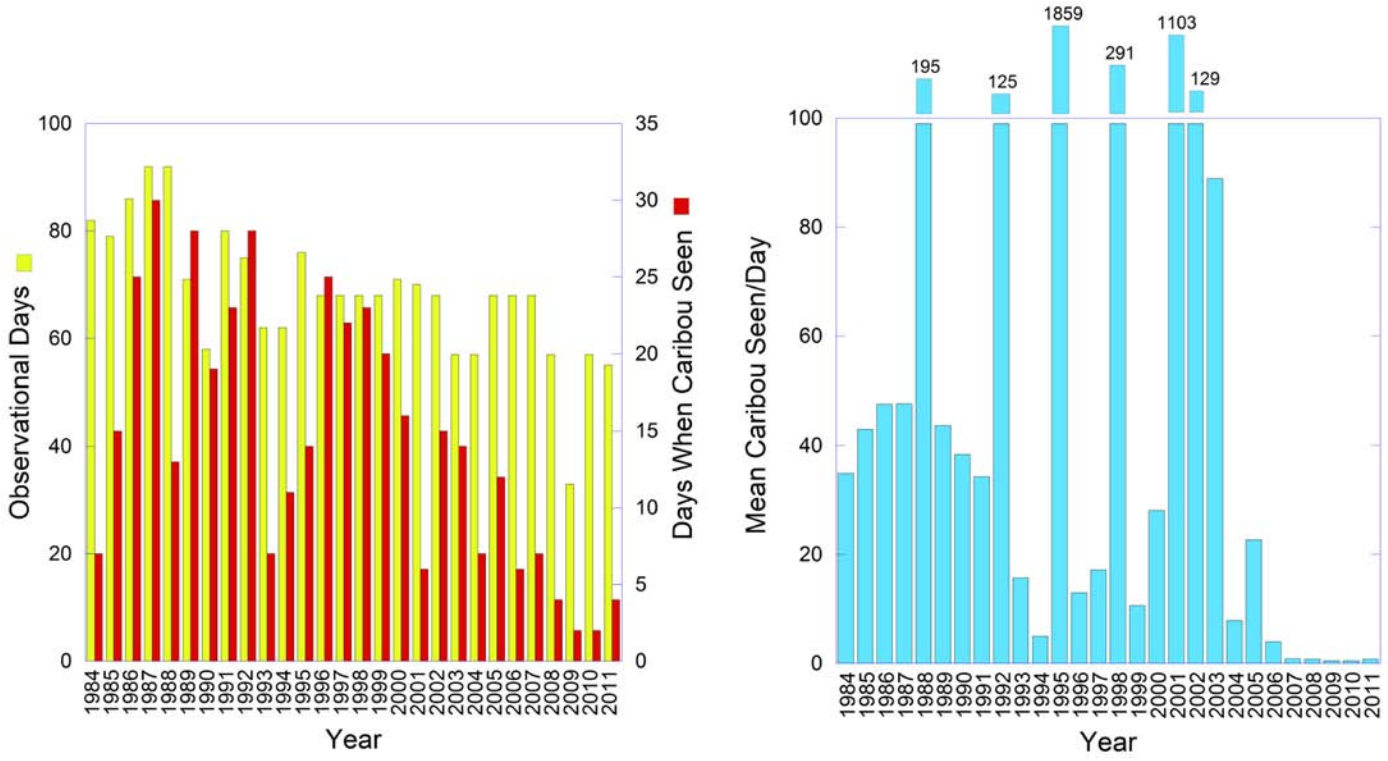


FIG. 7. (Left) Number of observation days (yellow) and days on which caribou were seen (red) during Alex Hall's Thelon River trips in 1984–2011. (Right) Number of caribou seen per day on days when caribou were observed (excluding largest group), from Alex Hall's Thelon River trips in 1984–2011.

Bluenose-East herds in 2005–13 (Davison et al., 2014). We suggest that the much higher exchange rates observed for collared Beverly cows in 2006–09 were likely an exception to the normally high fidelity documented previously in this herd and in other regional herds.

Earlier studies of the Beverly herd into the 1990s show a longstanding consistent use of calving grounds (Gunn and Sutherland, 1997), traditional water crossings (Gordon, 1996, 2005), and seasonal ranges (Heard, 1983; Thomas et al., 1998). Calving by Beverly cows to the south of Beverly Lake on their migration north was known for this herd in years of late spring and late snowmelt (Fleck and Gunn, 1982; Gordon, 2005) and likely occurred in 1993. Calving south of traditionally used calving grounds in years of late snowmelt and spring has also been observed in the Porcupine and Western Arctic herds (Alaska Department of Fish and Game, 2011).

The number of Beverly caribou that shifted calving grounds between 2007 and 2009 is difficult to estimate given the limited data from collars and surveys. By 2007, abundance of breeding females was already low (hundreds) on the traditional Beverly calving ground; on the Ahiak calving grounds, densities of caribou were much higher but declined 60% between 2006 and 2009 (Adamczewski et al., 2009), making a large-scale influx of Beverly caribou to the Queen Maud Gulf coast unlikely at that time. An extreme numerical decline in the Beverly herd could have resulted in a shift in use of calving grounds so that the few remaining Beverly cows calved among the more abundant Ahiak cows on the coastal Queen Maud Gulf calving grounds and adopted the Ahiak herd's seasonal ranges. As a result of the spatial shift by Beverly cows and concurrent use of the coastal calving grounds by both herds, the Beverly herd was no longer identifiable as a distinct herd.

The alternative explanation for the decline and disappearance in caribou on the inland Beverly calving ground is that this trend is primarily accounted for by a distributional shift by Beverly cows to the calving distribution in Queen Maud Gulf that is also used by the Queen Maud Gulf (Ahiak) subpopulation (Nagy et al., 2011). The Beverly shift likely began in the mid-1990s (Nagy et al., 2011). Under this explanation, the Beverly herd remains an identifiable subpopulation calving in Queen Maud Gulf, along with a Queen Maud Gulf subpopulation that shares a calving ground with the Beverly herd. Nagy et al. (2011) identified three patterns of calving ground use among the collared caribou using this area: E-1 coastal, F traditional, and F to E-1 traditional to coastal. A June 2011 survey by Campbell et al. (2012) provided estimates of 124 200 ± 14 000 adults in the Beverly subpopulation and 71 340 ± 3880 in the Ahiak (Queen Maud Gulf) subpopulation. These numbers indicate a decline from previous estimates for these caribou, regardless of whether they are assumed to be Ahiak, Beverly, or Ahiak+Beverly (Campbell et al., 2012).

Our analysis of the same collared caribou using the Beverly (traditional) and Ahiak (coastal) calving grounds concurs on the shift of a number of Beverly cows to the north during 2006–09 and on the convergence of movements of

Switched (traditional-to-coastal) cows with those of Ahiak (coastal) cows after 2007. We acknowledge that the monitoring gaps hamper determining definitively when Beverly caribou first began to switch fidelity away from their traditional calving grounds. However, we found no support for a shift in calving and other ranges of Beverly caribou prior to 2006, and the evidence for two subpopulations sharing the Queen Maud Gulf calving distribution (Nagy et al., 2011) was weak (Gunn et al., 2013a). Nagy et al. (2011) did not give a reason for a Beverly range shift but suggested that the Beverly shift to calving on the coast was similar to that of the Bathurst herd during the 1980s and 1990s because the distances were similar. However, the Bathurst calving shift was a progressive, directional shift from 1984 to 1996, with variable levels of overlap between consecutive calving distributions and no evidence for simultaneous use of two well-separated calving grounds (Gunn et al., 2012). If the Beverly cows started to shift to the coast in the mid-1990s (Nagy et al., 2011) to join Queen Maud Gulf or Ahiak caribou, then they also continued to calve approximately 250 km to the south on the traditional inland calving grounds in at least 2002 and between 2006 and 2009 (Johnson and Mulders, 2009; Campbell et al., 2012). We are unaware of any examples of a herd maintaining two geographically separate calving grounds 250 km apart over a 15-year period.

Overall, we suggest that the evidence gives strongest support to a steep decline in the Beverly herd followed by a shift of the remnant herd to calving in the coastal areas along Queen Maud Gulf, which were being used by a numerically more abundant Ahiak herd. Productivity and cow survival in the Beverly herd were exceptionally low between 2007 and 2009, and both the rate of decline from 2002 to 2007 and demographic indicators paralleled declines in five regional herds from Inuvik to Queen Maud Gulf during this period (Adamczewski et al., 2009). In the Cape Bathurst, Bluenose-West, and Bathurst herds, surveys either in late winter or on the calving grounds suggested a period of widespread adverse environmental conditions between 2000 and 2006, possibly weather and range mediated, signaled by late calving, low calf productivity, and a declining natural trend (Adamczewski et al., 2009). The limited Beverly data suggest a similar and possibly more severe effect over the same period. Earlier estimates of Beverly cow fidelity to annual ranges were 94%–98% from the 1960s to the 1980s, similar to rates documented from collars in several other regional herds. The 28% calving ground fidelity in collared Beverly cows and 31% probability of movement to the Ahiak calving ground between 2006 and 2009 may represent the low number of cows remaining on the Beverly traditional calving ground, but they are unlikely to be typical of a healthy Beverly herd at more substantial numbers.

A plausible mechanism consistent with the extremely low caribou densities on the Beverly calving grounds and low adult survival and productivity from 2007 to 2009 is a collapse in gregarious calving, which resulted in the greatly reduced numbers of Beverly cows joining much larger numbers of cows from the Ahiak herd and migrating 250 km farther north to maintain the advantages of gregarious calving and enhance predator avoidance (Gunn et al., 2012). Information on predation rates is limited, although predator sightings on the traditional calving grounds were high. During Beverly calving reconnaissance surveys in June 2007, four grizzly bears (*Ursus arctos*) and seven wolves were seen per 100 flying hours; comparable numbers for the June 2008 survey were eight bears and 18 wolves (Poole et al., 2014).

The only comparable information is from 1994 when Williams (1995) recorded 54 wolves and 11 grizzly bears per 100 flying hours. It is likely that the June 2007–09 calf:cow ratios on the Beverly calving ground were related partly to low pregnancy rates, but also to low early calf survival, which may have decreased from 2007 to 2009. A shift in calving ground fidelity at very low numbers would be consistent with cows' reducing predation risk during calving (Bergerud at al., 2008).

*Conservation Implications*

Here we have examined available data to interpret the underlying demographic processes that likely resulted in a steep decline of the Beverly herd, which we believe led to a loss in calving ground fidelity and a subsequent shift by the remaining breeding females to calving grounds ~250 km north in the coastal lowlands of Queen Maud Gulf. Despite the limited data and monitoring gaps, our interpretation is plausible and has several implications for wildlife conservation and management.

First, Aboriginal people and caribou have shared the annual range of the Beverly herd for about 8000 years (Gordon, 1977, 1996, 2005). The Beverly herd may have been one of the main herds with a "center of habitation" (Skoog, 1968; Bergerud et al., 2008) that persisted on the landscape for extended periods. The herd's disappearance from traditional ranges may be an exceptional event.

Second, loss of a subpopulation is considered a troubling signal for conservation. It has rarely been documented among barren-ground caribou in recent times. In Alaska, two larger and increasing herds of mountain caribou (Delta and Mulchatna) expanded their calving ranges and overlapped the nearby (< 25 km) calving distribution of smaller and declining herds (Yanert and Kilbuck) in the late 1980s and early 1990s, apparently absorbing the smaller herds (Valkenburg and Davis, 1986; Hinkes et al., 2005). Over a longer time span of 150 years leading up to the 1960s, Skoog (1968) concluded from historic evidence that small herds in Alaska shifted ranges and at times disappeared from formerly occupied ranges, while main subpopulations at the "center of habitation" usually persisted over long periods through times of caribou scarcity.

Third, assessing the Beverly herd's likely fate by evaluating alternative explanations with all available data is a reminder that a false conclusion, i.e., concluding a

substantial numerical decline in caribou abundance did not occur when in reality it did, is the more serious error because it may result in long-term harm to the resource. The alternative error is concluding that a numerical decline had occurred, when in reality the herd was numerically stable or had undergone a widespread change in distribution, or both; this error could result in imposing unnecessary conservation actions and harvest restrictions on hunters and resource users. If our assessment is correct, then a caribou herd estimated at 276 000 in 1994 declined to low numbers, abandoned its traditional ranges, and disappeared as a discrete herd within about 16 years. Gaps in monitoring and uncertainty over the herd's fate made timely management for recovery more difficult. In retrospect, continued monitoring after 1994 and enhanced monitoring after 2002 might have detected the decline sooner and allowed more timely actions to address the decline and foster recovery.

Finally, we should consider the possibility that calving caribou will return to the traditional Beverly calving grounds south of Garry Lakes. The three migratory caribou herds (Bathurst, Leaf River, and George River; Gunn et al., 2012; Taillon et al., 2012) that shifted calving grounds at peak densities moved to areas that had been unoccupied for decades but had a historical record of previous use (Bergerud et al., 2008; Gunn et al., 2012). As recommended by the Beverly and Qamanirjuaq Caribou Management Board (2004), the Beverly traditional calving grounds should still be protected from habitat loss through industrial development in case gregarious caribou calving should also reappear there.

## ACKNOWLEDGEMENTS

We would like to thank a number of biologists who contributed substantially to our collective understanding of the Beverly herd's ecology: Gerry Parker, Doug Heard, Mark Williams, Don Thomas, and Deborah Johnson. Studies by Bryan Gordon and colleagues extended our knowledge of caribou and their hunters in the Beverly range far back in time. We extend a very special thanks to Bonnie Fournier, Judy Williams, Adrian D'Hont and Leslie Wakelyn for the many patient hours of work building maps and other material for this report. We thank Tim Trottier for his support in helping us develop this paper. Chris Johnson in Prince George, BC, Mark Williams in Smithers, BC, and Suzanne Carrière in Yellowknife, NT, constructively reviewed earlier drafts of the manuscript. The three anonymous reviewers for this manuscript gave generously of their time and attention and we are grateful for their helpful comments and suggestions.

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