Modeling the decline of the Porcupine Caribou Herd, 1989–1998: the importance of survival vs. recruitment

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Abstract: The Porcupine caribou (Rangifer tarandus granti) herd increased from approximately 100 000 animals during the 1970s to 178 000 in 1989, then declined to 129 000 by 1998. Our objective was to model the dynamics of this herd and investigate the potential that lower calf recruitment, as was observed during 1991-1993, produced the observed population changes. A deterministic model was prepared using estimates of birth and survival rates that reproduced the pattern of population growth from 1971-1989. Then, parameters were changed to simulate effects of lower calf recruitment and adult survival. Reducing recruitment for 3 years caused an immediate reduction in population size, but the population began to recover in 5-6 years. Even a dramatic temporary reduction in recruitment did not explain the continuing decline after 1995. In contrast, a slight but persistent reduction in adult survival caused a decline that closely followed the observed pattern. This suggests that survival of adults, and perhaps calves, has declined since the late 1980s.

Key words: Alaska, population model, Rangifer tarandus.

ntroduction

The Porcupine caribou herd (PCH) has been the subject of a variety of research and monitoring efforts that began during the early 1970s, increased greatly during the 1980s, and has continued at a reduced level since 1994 (Griffith et al., 2002). Throughout this period, a series of surveys were conducted to estimate population size by counting caribou on aerial photographs taken during the post-calving period. In addition, research during the 1980s provided estimates of parturition, survival, and sources of mortality of calves and adults (Fancy et al., 1989, 1994; Fancy & Whitten, 1991; Whitten et al., 1992). Since 1994, fieldwork has been focused primarily on estimating parturition rates and survival of calves during June, photographic population estimates at intervals of 2–4 years, and estimating the age and sex composition of the herd during late winter (Stephenson, 1999). Some additional data have

been collected regarding body condition and the occurrence of diseases (Farnell et al., 1999).

During this period, the PCH increased from approximately 100 000 caribou in 1970 to 178 000 in 1989. From 1990–1998, the herd declined at a rate of 3–4% per year, and was estimated at 129 000 in 1998 (Stephenson, 1999). No measure of sampling variability is available for these surveys; thus, it is not possible to estimate confidence levels for the presumed changes among years. However, identical methods were used for all surveys, and the decline was consistent across surveys from 1989–1998, contrary to what would be expected if differences were due to random errors. Thus, we assumed that the indicated trend did exist, and that the magnitude of the decline was similar to what the surveys suggested.

From 1990–1993, a series of environmental events occurred that greatly reduced calf recruitment, as

Table 1. Summary of demographic data for the Porcupine Caribou Herd, 1987-2000. Data are from Fancy et al. (1994), Alaska Department of Fish and Game (unpubl.) and Yukon Department of Environment (unpubl.).

Year	Cows Observed[a]	Parturition Rate (%)	June Calf Survival[b]	1 July Calf:100 Cows[c]	Population Estimate[d]
1987	51	78	71	55	165 000
1988	91	84	65	55	
1989	74	78	74	58	178 000
1990	74	82	90	74	
1991	74	74	82	61	
1992	78	86	57	49	160 000
1993	63	81	56	45	
1994	98	91	77	70	152 000
1995	95	69	86	59	
1996	74	89	81	72	
1997	48	75	77	58	
1998	58	83	82	68	129 000
1999	39	84	83	70	
2000	44	73	60	44	
Mean	69	81	74	60	

[a] Number of radiocollared cows for which parturition status was determined. Parturient cows include those seen with calves and those judged to be pregnant or to have recently given birth to a calf that was not seen (Whitten, 1995).
[b] Estimated as July calf:cow ratio divided by parturition rate.
[c] Includes only radiocollared adult cows ≥3 years old.
[d] Total population estimated from photographic counts.

indicated by estimates of parturition and survival during June. Deep snow on the herd's winter range during the winter of 1990–1991 was followed by a reduced parturition rate during 1991. The following winter was relatively mild, but persistent snow cover delayed spring migration. The summer of 1992 was short and cool, influenced by lingering effects of the eruption of the Mt. Pinatubo volcano the previous year. Although parturition was relatively high in 1992, calf survival during June was low. The winter of 1992-1993 was again characterized by deep snow, and parturition rate was low during 1993. The combined effect of this series of events was that the ratio of calves:100 cows during July 1993 was the lowest recorded during the 1990s (Table 1).

Soon after the decline began, two modeling studies were published wherein the authors attempted to evaluate potential causes of the decline. The first of these (Fancy et al., 1994) used a deterministic spreadsheet model based on birth and survival rates that had been estimated from radiocollared caribou. The second study (Walsh et al., 1995) used a stochastic model to evaluate potential effects of changes in birth rate and calf survival on herd size. Both of these models were sensitive to changes in adult survival rates and calf recruitment. Because reported harvest levels had not increased and measures of win-

ter body condition remained relatively high, it was believed that changes in the population were largely influenced by reduced recruitment, although small changes in adult survival might also have contributed to the decline (Fancy et al., 1994). This was thought to be a temporary condition that would be reversed as the larger cohorts produced after 1993 entered the adult population (International Porcupine Caribou Board, 1998). However, despite favorable weather and increased rates of parturition and early calf survival from 1994–1998 (Table 1), the decline continued. Thus, our objective was to model the dynamics of the PCH to evaluate whether 3 years of reduced recruitment could account for the observed decline, or if some other change might have occurred.

Methods

Fancy et al. (1994) estimated parturition rates and survival of radiocollared calves (1983–1985 and 1988) and adults (1982–1991) of the PCH using the staggered entry product-limit method of Pollock et al. (1989). We used similar methods to estimate survival of radiocollared adult females during 1997–2001. However, beginning in 1993, calves were not radiocollared and radiocollared adult caribou were
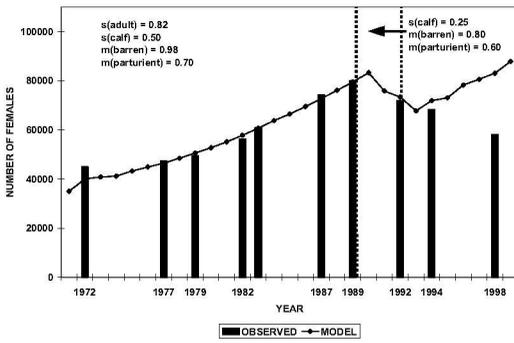
Fig. 1. Observed and predicted changes in population size of female Porcupine caribou, 1971–1999. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model using the specified parameters for survival (s) and birth rate (m), with a reduction during 1991-1993. Birth rates differ depending on parturition status during the previous year (barren or parturient).
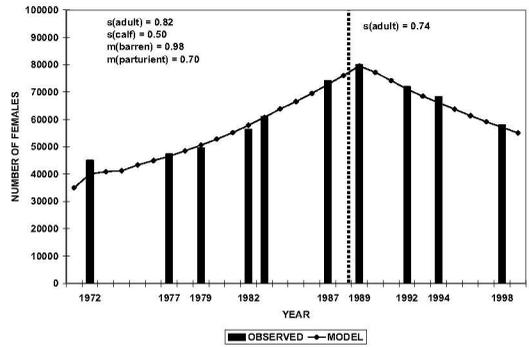

Fig. 2. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of adults was reduced during 1990–2001. Birth rates (m) differ depending on parturition status during the previous year (barren or parturient).
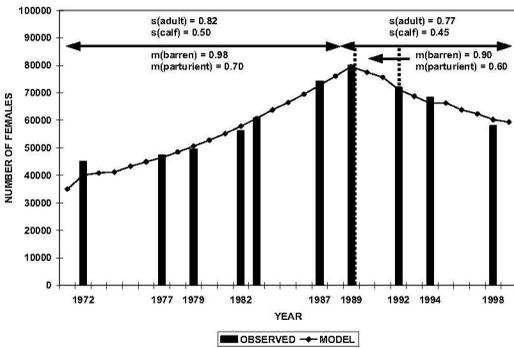

Fig. 3. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of adults was reduced during 1990–2001 and birth rates (m) were reduced during 1991–1993. Birth rates differ depending on parturition status during the previous year (barren or parturient).
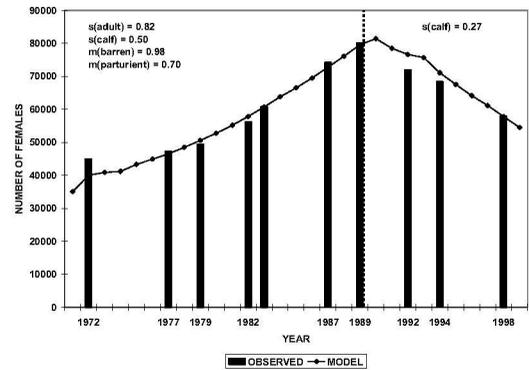

Fig. 4. Observed and predicted changes in population size of female Porcupine caribou. Observed data are from photographic counts, assuming adult females were 45% of the herd. Predicted data are from a model where survival rate (s) of calves was reduced during 1990–2001. Birth rates differ depending on parturition status during the previous year (barren or parturient).

located less frequently, so annual survival rates could not be estimated as precisely as in earlier years. Because of infrequent radio locations, we assigned deaths only to the year in which they occurred (year = 1 June–31 May). Even so, there were relatively large numbers of censored animals during some years. Most of these likely had died (many deaths were confirmed later) but the year in which these deaths occurred could not be determined. To partial-

ly accommodate this problem, we determined a maximum estimate of survival by eliminating censored data beginning with the period following an animal's last location (assumes that cause of censoring was not related to survival) and a minimum estimate by assuming that censored animals had died during the year following their last location. Because both of these extremes likely are inaccurate (death was a likely cause of censoring, but not all censored ani-

Table 2. Estimates of annual survival for radiocollared adult female caribou of the Porcupine Herd, 1997–2001. Rates were estimated for 1-year periods ending 1 June of the year indicated using the staggered entry design of Pollock et al. (1989).

Year	Censored animals eliminated[a]						Censored animals counted as deaths[b]			Mean[e]
	At risk	Deaths	Censored[c]	Survival	Upper CL[d]	Lower CL[d]	Survival	Upper CL[d]	Lower CL[d]	
1997	58	0	8	1.00			0.88	0.95	0.80	0.94
1998	51	2	22	0.96	1.00	0.91	0.67	0.76	0.58	0.82
1999	52	10	14	0.81	0.90	0.71	0.64	0.73	0.54	0.73
2000	39	6	16	0.85	0.95	0.74	0.60	0.70	0.50	0.73
2001	48	5	5	0.90	0.98	0.81	0.81	0.91	0.72	0.86
Mean				0.90			0.72			0.81

[a] Assumes that censoring is not related to survival.
[b] Censored animals are added to numbers at risk and numbers of deaths.
[c] Fate or year of death was unknown.
[d] Upper and lower 95% confidence limits on survival estimate.
[e] Mean of survival estimates with and without censored animals.

mals had died), we chose the mean of these estimates as our best estimate of survival.

We then constructed a deterministic spreadsheet model similar to the one used by Fancy et al. (1994). The major differences in the models were that ours considered only the female segment of the population, and we used 2 different rates of parturition, so that females that produced a calf in 1 year had a lower parturition rate during the following year. This modification was suggested by data that indicated an alternate-year fluctuation in parturition rate by the PCH (Table 1). Such a pattern is a consequence of multi-year reproductive cycles (Gilbert & Udevitz, 1997) when periodic reproductive failures synchronize breeding among individuals. A similar effect can be produced in populations that reproduce annually, if probability of parturition differs depending on reproductive success during the previous year (this study). As is the case with multi-year reproductive cycles, the alternate-year fluctuations are most noticeable following years when reproductive success is temporarily reduced, and gradually dampen out when reproductive rates are near the long-term mean. The initial population was established using the stable age distribution calculated by Walsh et al. (1995), assuming that females ≥1 year old were 45% of the population (International Porcupine Caribou Board, 1990). The initial population size was determined so as to approximate the observed changes in population size during 1970–1989 (Fig. 1). The model assumed that no caribou produced a calf until age 3 and that parturition of caribou aged ≥3 was equal to 1 of 2 rates, depending on reproductive success the previous year. Caribou were assumed to live a maximum of 12 years, and separate survival rates were used for calves and for caribou aged 1–11 years. Fancy et al. (1994) reported higher survival for caribou aged 1–2 years compared to those aged ≥3 years. However, these authors believed that survival rates of 1- and 2-year old caribou in their study likely were overestimated, due to small annual samples and the number of censored animals. Thus, we used one survival rate for all caribou aged ≥1 year.

After the initial model was constructed, various input parameters were changed to determine the magnitude of changes that would be necessary to duplicate observed changes in population size. First, we reduced parturition rate and annual calf survival during 1991–1993 to produce a population decline similar to what was observed from 1987–1994. These rates were restored to their initial levels beginning in 1994. Next, we modeled the population using constant rates for parturition and calf survival, but with reduced adult survival beginning in 1990 and persisting for the duration of the model period.

Table 3. Estimates of initial productivity (calves/100 cows during mid–late June) of caribou herds in arctic Alaska, 1987–1998.

Year	Western Arctic[a]	Teshekpuk[b]	Central Arctic[c]	Porcupine[d]
1987	74		74	55
1988	81		66	55
1989	78		48	58
1990	72		75	74
1991		66	45	61
1992	86	80	73	49
1993	54	39		45
1994	72		65	70
1995	59	73	50	59
1996	61			72
1997	57	46	72	57
1998	53	67		68
Mean	68	62	63	62

[a] Data from mid June; counts of calves may be higher due to less calf mortality and the inclusion of some pregnant cows (Dau, 1999).
[b] Data from post-calving (Carroll, 1999).
[c] Data from post-calving (Lenart, 1999).
[d] Data from post-calving (Stephenson, 1999).

For the third model, we altered parturition, calf survival, and adult survival. As in the first modification, parturition and calf survival were reduced only during 1991–1993, but adult survival was reduced in 1990 and then held constant for the duration of the period modeled. Finally, we reduced calf survival during 1990 by an amount sufficient to duplicate the observed population decline, and maintained that rate for the duration of the model period. In all cases, attempts were made to approximate the observed changes in population size by manipulating the specified parameters.

Results

From 1982–1992, mean annual survival rates of adults and calves were 0.84 and 0.51, respectively, and mean parturition rate was 0.80 for cows aged ≥3 years (Fancy et al., 1994). From 1997–2001, mean annual survival of adults was 0.90 if censored animals are removed and 0.72 if censored animals are assumed to have died. Annual means of these extremes ranged from 0.73–0.94, and the mean over all years was 0.81 (Table 2).

For our initial model, we used parturition rates of 0.98 and 0.70 for 3-year-old and older cows that were barren or parturient, respectively, during the previous year. These rates produced a parturition rate of 0.80 for all adult females. This model required survival rates of 0.82 and 0.50 for adults and calves, respectively, to match the observed rate of increase during this period. These rates were within the 95% confidence limits reported by Fancy et al. (1994) and the rate for adults was similar to the mean of our minimum and maximum estimates of adult survival from 1997–2001. The predicted growth of the PCH based on this model closely matched the observed counts from 1972–1989 (Fig. 1). Reducing parturition rates during 1991–1993 to 0.60 and 0.80 for cows that either did or did not produce a calf during the previous year produced annual parturition rates of 0.68–0.70 for all adult females, similar to the lowest parturition rate observed during 1991–1993 (Table 1). This model required a calf survival rate of 0.25 to produce a decline similar to that observed between 1989 and 1993. However, the model population began to increase within 2 years after parturition and calf survival rates were restored to previous levels, and had exceeded 1989 levels by 1998 (Fig. 1). In contrast, reducing adult survival to 0.74 starting in 1990 caused the model population to decline in a pattern that closely matched the observed decline through 1998 (Fig. 2). Similarly, reducing adult survival to 0.77, calf survival to 0.45 (both beginning in 1990) and parturition from 1991-1993 to 0.60 or 0.90 (for cows previously parturient or not parturient, respectively) also caused a decline similar to what was observed (Fig. 3). Reducing calf survival to 0.27 while holding the other parameters constant caused the population to decline but the slope and timing of the decline differed from what was observed (Fig. 4).

Discussion

Our intent was not to estimate true values of model parameters, but to evaluate different scenarios that might have led to the observed population decline. Thus, none of the simple models that we developed can be expected to accurately represent the dynamics of the population. However, our results strongly suggest that, in the absence of any other changes, a reduction in recruitment much greater than what was thought to have occurred during 1991–1993 would have been necessary to produce the initial decline shown by the PCH. Furthermore, the effects of this reduction would have been short-lived. Although changes in parturition and calf survival through June were recorded during the early 1990s, we have no data to suggest that these were accompanied by changes in calf survival through the remainder of the year. If calf survival were reduced substantially (e.g., by 50% as in our model), then the observed reductions in birth rate and initial survival might have been sufficient to cause the decline shown by the PCH during the early 1990s. However, unless calf survival remained low, the herd should have recovered to former levels by 1998.

Conversely, a relatively small but persistent change in adult survival could have produced the observed population decline. When combined with a 3-year reduction in recruitment, only a 6% reduction in adult survival was necessary to duplicate the observed decline, and the survival rate necessary to produce this effect was greater than our minimum estimate of adult survival during 1997–2001. This conclusion is supported by other studies that have demonstrated the sensitivity of ungulate population growth rates to small changes in adult survival (e.g., Nelson & Peek, 1984; Eberhardt, 1985; Hern et al., 1990; Crête et al., 1996; Walsh et al., 1995).

Depending on whether censored animals are excluded or counted as deaths, estimated adult survival during 1997–2001 was either greater or less than survival during 1982–1992. This illustrates some of the difficulty involved in detecting relatively small changes in adult survival in a herd with a range as large as that of the PCH. Even if there were no censored animals, it would be difficult to detect small changes with any statistical precision. For example, Walsh et al. (1995) estimated that for samples of 100 radiocollared caribou, there was only an 80% chance of detecting changes in survival rates of ≥24% at the 95% confidence level. Even if the radio-tracking effort were doubled, changes as small as 5–10% would be difficult to detect.

Potential causes of increased adult mortality include density-dependent nutritional effects, disease, and losses to predation and human harvest.

Condition indices of harvested and live-captured caribou did not suggest that PCH caribou were under nutritional stress (Yukon Department of Environment and Alaska Department of Fish and Game, unpubl. data), and the incidence of common disease agents in the PCH was relatively low (Farnell et al., 1999). Although accurate data on predator populations are not available for the PCH range, observations of wolves and lynx increased during the 1990s in much of the area (U.S. Fish and Wildlife Service, unpubl. data). Conversely, during this period populations of moose declined by as much as 75% in the western half of the herd's summer and winter ranges (Stephenson, 1998). Snowshoe hares (*Lepus americanus*) in interior Alaska increased during the 1990s (McIntyre & Adams, 1999; Alaska Department of Fish and Game, unpubl. data). This increase was correlated with increased nesting success by golden eagles (McIntyre & Adams 1999). Radio-tagged immature eagles dispersed from the Alaska Range to the PCH calving grounds on the Arctic coastal plain (C.L. McIntyre, U.S. National Park Service, pers. comm.), where eagle predation was the major cause of calf mortality (Whitten et al., 1992). Thus, predation on caribou likely was high and may have increased during the 1990s. Reported human harvests have fluctuated between 2000 and 3000 caribou, and did not increase during the 1990s (International Porcupine Caribou Board, 1995; Stephenson, 1999; Yukon Department of Environment, unpubl. data). This was only 1.5-3.0% of the estimated population. However, unreported harvest and wounding losses were unknown. Other modeling efforts (Hayes & Russell, 2000; Hanley & Russell, 2000) suggested that, considered separately, neither wolf predation nor human harvest was likely to limit the PCH at current levels. However, these models did not consider potential combined effects of hunting, high predation, and reduced recruitment.

Compared to other caribou herds in arctic Alaska, the maximum observed rate of increase of the PCH is relatively low (4.9% during 1979–1989, vs. 9.5, 13.0, and 10.3 % for the Western Arctic, Teshekpuk Lake, and Central Arctic herds, respectively [Griffith et al., 2002]). Reasons for this difference are unknown, but annual estimates of initial productivity (parturition rates and June calf:cow ratios) for the PCH were generally similar to estimates for the other herds (Table 3), suggesting that mortality was higher for the PCH, even during periods of population growth. We recommend that future management and research concerning the PCH should direct more effort towards estimating survival rates and the relative importance of various mortality factors.

Acknowledgements

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