PROJECT TITLE: DYNAMICS OF THE DENALI CARIBOU HERD, DENALI NATIONAL PARK, ALASKA: PROGRESS REPORT (OCTOBER 2014 - SEPTEMBER 2015)

INVESTIGATORS: Layne G. Adams, USGS-Alaska Science Center, 4210 University Drive, Anchorage, AK 99508

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Population dynamics of the Denali Caribou Herd have been studied continuously at Denali National Park since 1984. Denali National Park (18,800 km^2) encompasses nearly the entire range of the Denali Herd, thus providing a unique opportunity to investigate caribou population dynamics where ungulate populations (caribou, moose, and Dall's sheep) and the large carnivores that prey on them (wolves, grizzly bears, and American black bears) are driven primarily by natural processes.

To date, much has been learned about the interactions between predation and weather that determine the dynamics of the Denali Herd. In the mid-1980s, the herd was increasing at about 7%/year during a long period of relatively mild winters. Survival of caribou cows was high (96%/year) and about 50% of the calves produced were recruited in autumn. With the onset of several consecutive severe winters in 1988, caribou numbers leveled off at 3,200 by fall 1989, and then declined by nearly a third to 2,300 caribou over just 3 years**.** During the decline, adult cow survival dropped substantially, to an average of 85%/year, and calf recruitment fell to about 10%. During 1993-2003, with a return to moderate winter snowfall, adult female survival returned to high levels but fall calf recruitment remained low, averaging 15%. As a result, the herd continued to decline but a much slower rate of about 2% annually. With prolonged low calf recruitment, the female age structure became heavily weighted towards older females, a harbinger of impending population declines regardless of winter snowfall patterns if calf survival remained low. In May 2002, the proportion of females that were ≥ 13 years old peaked at 24%. As a result of these old females dying, adult female survival was low in the 2002-03 and 2003-04 winters (average = 83%) even though winter snowfalls were substantially below average. These survival rates were comparable to rates measured during the extreme winters of 1990-93. However, at about the same time, we noted a marked increase in calf survival that offset these high cow losses. During the last 12 years (2004-2015), calf survival to fall has improved, averaging 28% annually, allowing for limited growth of the herd through 2013 of about 2% per year. Although the current herd estimate is preliminary, very high winter survival of adult females (> 98%) during the last 2 winters with little snowfall appears to have resulted in population increases of 10% per year.

In addition to basic population monitoring, I have been investigating patterns of growth, survival and seasonal distribution of male caribou since 2007. In general, little is known about the population ecology of male caribou because research and monitoring efforts are commonly focused on adult females and their dependent young given that these sex/age classes tend to drive population trends. Although prior to

these studies little was known about male mortality of Denali caribou, 2 interesting and unexpected patterns arose from investigations of wolf kills in Denali during 1986-93. First, large male caribou showed up in the wolf kill primarily in August and September prior to the annual rut, when caribou bulls should have been in peak condition. High mortality following the rut resulting from the deteriorated nutritional condition of breeding males was expected, but such pre-rut mortality was not. Also, the wolf kill data indicated that mortality of caribou males unexpectedly ended in mid-winter. These patterns have been corroborated with 78% of the observed mortality of adult males occurring during July – November, and few mortalities detected in late winter (February – April; 4%).

The current goals of caribou studies in Denali are: 1) to document population trends, primary vital rates (calf production, calf recruitment, adult female survival), and other important population characteristics (female age structure, adult sex ratios) that determine the status of the Denali Caribou Herd, and 2) to evaluate growth, survival and seasonal distribution of adult males. This progress report summarizes research and monitoring of the Denali Caribou Herd conducted during October 2014-September 2015 (FY15). During this period, the specific objectives included:

1. Estimate the population size and composition in late September each year;
2. Determine productivity, survival patterns and age structure of adult females;
3. Assess calf production and recruitment;
4. Investigate the patterns of growth, survival, and seasonal habitat selection of male caribou;
5. Relate caribou population status, trends, and vital rates to climatic variables and predator population characteristics.

METHODS

Capture and Radiocollaring

Female caribou are captured by helicopter darting and radiocollared to monitor their survival, productivity and movements, and to aid in conducting composition surveys and herd counts. I have maintained an age-structured sample of approximately 60 females ≥ 1 year old by recruiting yearling females annually relative to the ratio of female calves to adult females in the herd in the previous September, and by recollaring individuals surviving in the sample every 4 years, prior to exhaustion of radiocollar batteries. Each March, I instrument 12 female calves (10-months-old) to provide recruits for the age-structured sample and to monitor productivity of young age-classes (2 and 3 years of age) that exhibit much of the variation in productivity observed in females overall. Females captured as 10-month-olds but not recruited into the age-structured sample have their collars removed at about 4 years of age to limit the number of radiocollared caribou.

Adult bulls were initially captured in mid-September 2007 to establish a sample of about 50 radiocollared individuals; additional bulls were captured in 2008-2013 as needed to maintain that sample. In addition, 12 10-month-old male calves were radiocollared each year in March 2008-2012 to investigate growth patterns and survival of young bulls. These individuals are recaptured at 4 years of age and subsequently

included in the sample of adult bulls. In September 2014, we replaced VHF radiocollars on 20 bulls with GPS collars that acquire and store locations every 2 hours for 3 years to investigate fine-scale habitat selection of males. We instrumented an additional 19 bulls with GPS collars in September 2015. These collars are designed to drop off surviving caribou after 3 years (September 2017 or 2018).

Caribou captures generally occur in March for females and calves, and mid-September for adult bulls. Currently, we are using a mixture of carfentanil citrate and xylazine hydrochloride for immobilizing caribou, with specific doses for adult females, adult males, and 10-month-olds. A PA-18 Supercub working with the helicopter locates caribou for darting, monitors darted caribou during induction, and checks on caribou captured on previous days. Once a caribou is immobilized, it is fitted with a mortality-sensing radiocollar, standard body measurements are taken, and a blood sample is drawn for disease screening. All caribou are weighed to the nearest 0.5 kg. A canine tooth is extracted for age determination from all adults on their first capture. Once processing is completed, caribou were given naltrexone hydrochloride and yohimbine hydrochloride to antagonize the effects of carfentanil and xylazine, respectively.

Radiotelemetry: survival and seasonal distribution

All radiocollared caribou are relocated by aerial radiotracking from fixed wing aircraft approximately every 2 months throughout the year to determine their distribution and survival. In addition, caribou are located to assess natality (mid-May at approximately the peak of calving), and to aid in composition surveys and the annual census (early June, late September). Thus the annual radiotracking schedule is as follows: mid-May (natality assessment by observing calves at heel or distended udders); early June (post-calving composition survey and census); late July; late September (fall composition survey); late November; late-January; mid-March; and end of April. In addition, all radioed males are monitored every 2-3 weeks during August – October to refine estimates of the timing of adult male mortality. We attempt to observe mortalities from the radiotracking aircraft during monitoring flights and investigate by helicopter as soon as practical. Survival rates are calculated using Kaplan-Meier staggered-entry methods.

Pregnancy assessment

In mid-May, near the peak of the annual calving period, all radiocollared cows ≥ 2-years-old are located by radiotracking from a helicopter and observed to assess their pregnancy status based on a calf at heel, udder distension, or hard antler presence. During these surveys, the helicopter crew works with a Supercub that radiolocates caribou in advance of the helicopter to increase efficiency of the overall effort.

Composition surveys

I conduct 2 helicopter surveys to assess the age/sex structure of the herd annually. During these surveys, a predetermined search area, based on the distribution of radiocollared caribou immediately prior to the survey, is intensively searched and all caribou encountered are approached at close range with a helicopter and classified into

a small hand-held tape recorder. In early June following the calving season, caribou are classified as calves, cows, and bulls to determine a calf:cow ratio as an assessment of early calf survival. As mentioned below, this survey also serves as the basis for population estimates. The fall composition survey is conducted near the end of September at about the peak of the rut, to determine calf:cow ratios, calf sex ratios, bull:cow ratios. During this survey, calves are differentiated by sex and bulls are classified into 3 size classes (small, medium, and large; Table 1) based on body size and antler development.

Population estimation

Annual herd size is determined from on an estimate of the number of adult cows in the population based on postcalving survey results. Prior to that survey, the distribution of radiocollared adult females is assessed and a survey area delineated that ideally included > 67% of the marked females surrounded by a reasonable buffer defined by identifiable topographic features. The survey area usually consists of 2 to 4 large blocks of mountainous terrain along the main Alaska Range that take 1-2 days to fully survey. From a helicopter, we intensively search each survey block without the aid of radiotelemetry. Caribou groups encountered are counted and classified, and we determine the occurrence of marked individuals within groups via radiotelemetry. Simultaneously, a Supercub crew locates all radiocollared females in or adjacent to the survey block. Periodically through the survey as portions of a survey block are completed, we compare notes among the 2 aircraft crews to determine marked groups missed by the helicopter; those groups are then relocated by the helicopter and counted. In addition to adding these caribou to the totals counted, this information provided an assessment of sightability relative to group size during the survey. Because most cows and calves tend to be in large groups at this time of the year, sightability has generally been very high.

With the information collected, an estimate of the total number of cows in the herd is derived by dividing the number of adult females observed during the survey by the proportion of radiocollared adult females that were in the survey blocks. In addition to the estimate for a given year (t), I use available information on seasonal adult female survival from radiotelemetry, and calf sex ratios and calf recruitment from fall composition surveys to derive estimates based on counts of adult females in the previous (t-1) and subsequent (t+1) years, then use the mean of the 3 estimates as the estimated number of adult females for year t. Finally, I determine a fall population estimate by applying the adult female survival rate from radiotelemetry for June-September to estimate fall cow numbers, and fall herd composition to account for bulls and calves.

RESULTS

At the beginning of the fiscal year on 1 October 2015, we were monitoring 135 radiocollared caribou (82 females, 53 males). During the year, 8 bulls died of natural causes and 2 were harvested outside the park. We experienced 3 dropped collars and 2 failures, and removed 1 collar from a bull. Of the collared females, 5 died of natural

causes and 4 4-year-olds had their collars removed. In March 2015, we radiocollared 12 10-month-old female calves that survived to the end of the year. In September 2015, we deployed 8 GPS collars on bulls that were not previously collared. As a result, by 30 September 2015, we were following 130 radioed caribou (85 females, 45 males).

Herd Size

I derived a preliminary herd size estimate of 2,780 caribou for September 2015 (Table 1, Fig. 1); that number will be adjusted based on results of the 2015 census as described above. Although preliminary, the Denali Herd appears to have increased by about 10% per year since Autumn 2013. During these 2 years, winter snowfalls have been light and adult female survival over winter has been very high (> 98%). In addition bull:cow ratios have increased noticeably. Thus it appears, improved adult survival during these relatively easy winters for caribou have driven the observed increases in herd size.

Adult Sex Ratio

Based on classification of 1149 adult caribou on 1 October 2015, I derived an adult sex ratio of 47 bulls:100 cows (Table 1, Fig. 2B). Adult sex ratios declined from an average of 56:100 during 1984-1989 to a low of 29:100 during 1997-1998 as a result of increased mortality of males during severe winters in the late 1980s and early 1990s, as well as limited recruitment of male calves. Bull:cow ratios increased slowly through 2009 (36 bulls:100 cows), with greater increases since, particularly in the last 2 years. However, current adult sex ratios are still well below those at the beginning of the study.

Calf Production and Survival

Productivity of cows ≥ 1 year old was estimated at 76% in mid-May 2015, based on 72 radiocollared females in the age-structured sample (Table 2). Of the 9 cows other than yearlings that were not pregnant, most were either 2 years-old (n = 3) or ≥ 16 years-old (n = 3). Calf production has varied from 59% in 1990 to 92% in 1994 and is largely influenced by the number of yearling recruits, the highly variable productivity of 2-year-olds, and the proportion of older females in the herd.

During the mid-June 2015 postcalving surveys, we noted 39 calves:100 cows (Table 3), the highest postcalving calf:cow ratio since 1989. By 1 October, that ratio had declined to 24:100 (Table 1, Fig. 2A), near the average since 2004 (22.2:100). Based on these measures of calf production and survival, and accounting for adult female survival between mid-May and late September, survival to fall was estimated at 30% for 2015 calves (Fig. 3). Fall calf survival has averaged 28% over the last 12 years, compared to 42% and 15% during 1987-1990 and 1991-2003, respectively.

Female Survival and Age Structure

During October 2014-September 2015, we estimated an annual mortality rate of only 4% for adult females, lower than the long-term study average of 11% (range of annual values = 2-23%). Females ≥ 13 years old made up 11% of the population (Fig. 4, 5), declining from a recent peak of 22% in 2008. With continued moderate

recruitment, I expect the proportion consisting of these older females will continue to decline over the next few years because it is predominantly 15-17 year-olds that are nearing the end of their lives and there are few females 12-14 years old (2001-2003 cohorts that are the last from the period of very low recruitment) to come in behind them (Fig. 4).

Based on data collected from radiocollared females during October 1986 – September 2013, age-specific survival rates of females tend to be generally high for 2-7 year-olds, averaging 0.94, then decline slowly during 8-13 years of age prior to declining markedly as individuals become senescent (Fig. 6). The 2 oldest caribou females we have monitored died in May as they turned an estimated 20 years old.

Bull Growth Patterns

During September 2007-2015, we weighed 195 bulls ≥ 1 year old at their initial captures and recaptures to replace their radiocollars. In mid-September bull caribou should be at their maximum body for the year in preparation for the rut and ensuing winter. Overall, body masses of males ranged from 93 to 278 kg (Fig. 7). Body masses increased markedly with age from 1 to 6 years, gaining an average of 25 kg each year, and plateaued at 232 kg on average for bulls ≥ 6 years of age.

Adult Bull Survival

During September 2007- September 2015, we radiocollared and monitored 206 male caribou, including 145 captured as adults (≥ 1 year old) in mid-September, and 61 captured as 10-month-old calves (12-13 each March 2008-2012). We have experienced some difficulties with premature failure of radio-transmitters (*n* = 22) or loss of radiocollars (*n* = 30). In Fall 2010, we began deploying transmitters that were fully cast in urethane resin to protect the electronic components from shock during rutting fights. That appears to have reduced the failure rate. Many of the dropped collars (*n* = 20 of 30) have occurred during the rut in that they obviously were torn off during rutting fights; the collars are purposely designed to tear away if an opponent gets an antler tine caught under the collar. The remainder of dropped collars (*n* = 10) were due to premature failure of the elastic expansion sections in the collars. In addition to 5 capture-related deaths, we noted 102 deaths to natural causes including wolves (48), bear (15), accidents/avalanche (4), rut-related (3), unknown large predator (8), unknown (20), and unknown-not predation (4). The 4 unknown-not predation deaths occurred in October-November and I suspect they resulted from rutting injuries. During this reporting period, 2 bulls were harvested including 1 harvested near Cantwell in December 2014 and 1 killed near Haynes Lake, west of the park in September 2015.

During our studies of bull survival since September 2007, we have noted that age-specific survival rates were high for males 1-4 years-old, averaging 88% (Fig. 8). As bulls approached full adult size at 5 years of age and became active in the rut, their survival then declined to 78% and that level of survival continued through 6 and 7 years of age. After 7 years, survival dropped off markedly each year with very few caribou bulls surviving to 10 years. Interestingly, bulls ≥ 5 years old died predominantly during

July – November (83% of annual mortality) with nearly half this mortality (39% of annual mortality) occurring prior to the onset of the rut in mid-September (Fig. 9).

Movements and Habitat Selection

During September 2010-2013, we maintained a sample of 20 adult females instrumented with GPS collars that acquired and stored locations every 2 hrs. Those collars were retrieved in September 2013 and we are currently analyzing the mass of data collected. We deployed GPS radiocollars on 20 bulls in September 2014 and 19 bulls in September 2015. The bull collars are designed to automatically release after 3 years of data collection in September 2017 or 2018. The resulting data sets for females and males will be used to compare and contrast seasonal movements and fine-scale habitat selection patterns of the 2 sexes.

PLANNED ACTIVITIES (OCTOBER 2015 - SEPTEMBER 2016)

In the upcoming year, we will continue efforts to assess population dynamics of the Denali Caribou Herd while continuing to follow radiocollared bulls for additional survival data, as their GPS collars acquire locations for evaluating fine-scale habitat selection. Specifically, objectives for the year include:

1. Capture and radiocollar caribou females as needed to maintain an age-structured sample of approximately 60 individuals for estimation of calf production, age structure, survival patterns and seasonal distribution, and to aid in population monitoring.
2. Continue to monitor radiocollared bulls to provide additional data for estimating survival patterns of males ≥ 4 years old.
3. Locate all instrumented caribou in late November, late January, mid-March, late April, mid-May, early June, late July, and late September, or as needed to meet study objectives.
4. Conduct the post-calving census and composition survey and the fall composition survey to determine herd size, calf recruitment, and adult sex ratio.

Table 1. Results of helicopter composition surveys in late September and fall population estimates for the Denali Caribou Herd, Denali National Park and Preserve, Alaska, 1984-2015.

	Fall Survey Results											
				Ratios (:100 Cows)		Calf Sex Ratio	Bulls%[b]			Fall	Estimated Fall Herd Composition		
Date	Cows[a]	Calves	Bulls	Calves	Bulls	(m:100f)	S	M	L	Herd Size	Cows	Calves	Bulls
9/27/1984	375	154	184	41	49	--	--	--	--	2,200	1,158	475	567
9/25-26/1985	654	183	368	28	56	72	--	--	--	-	-	-	-
9/27/1986	547	210	305	38	56	--	--	--	--	2,470	1,272	488	709
9/25/1987	631	234	356	37	56	73	28	39	33	2,430	1,256	466	709
9/27-28/1988	678	221	451	33	67	70	27	34	39	2,950	1,482	483	986
9/28/1989	830	246	428	30	52	84	34	34	32	3,210	1,771	525	913
9/26-27/1990	777	130	387	17	50	59	39	28	33	3,100	1,861	311	927
9/26/1991	1,067	72	409	6.7	38	112	32	39	29	2,610	1,799	121	690
9/25/1992	643	103	282	16	44	66	31	40	29	2,340	1,464	234	642
9/27/1993	849	54	336	6.4	40	74	26	46	28	1,970	1,350	86	534
9/27-28/1994	648	128	253	20	39	88	21	38	41	2,140	1,348	266	526
9/25/1995	685	131	204	19	30	75	29	29	42	2,170	1,457	279	434
9/29/1996	820	103	243	13	30	69	32	26	42	2,060	1,449	182	429
9/26/1997	777	124	228	16	29	110	38	28	34	2,070	1,425	227	418
9/26/1998	718	87	205	12	29	98	41	27	32	1,790	1,272	154	363
9/29/1999	667	92	261	14	39	51	30	34	36	1,760	1,151	159	450
9/24-26/2000	730	52	257	7.1	35	86	32	31	37	1,930	1,356	97	477
9/27/2001	778	90	248	12	32	64	22	38	40	1,840	1,283	148	409
9/29/2002	453	72	145	16	32	76	22	17	61	2,050	1,386	220	444
9/30/2003	743	58	264	7.8	36	71	23	23	54	1,880	1,312	102	466
9/27/2004	774	214	309	28	40	69	19	30	50	2,120	1,265	350	505
9/26/2005	848	163	279	19	33	52	32	27	41	1,930	1,269	244	417
9/28/2006	691	145	269	21	39	59	30	29	41	2,090	1,307	274	509
9/28/2007	628	142	227	23	36	84	31	37	33	2,060	1,298	293	469

Table 1. Continued.

	Fall Survey Results												
				Ratios (:100 Cows)		Calf Sex Ratio	Bulls%[b]			Fall	Estimated Fall Herd Composition		
Date	Cows[a]	Calves	Bulls	Calves	Bulls	(m:100f)	S	M	L	Herd Size	Cows	Calves	Bulls
9/29/2008	677	152	222	22	33	85	32	30	38	2,070	1,333	299	437
9/28-29/2009	764	174	272	23	36	81	38	25	37	2,130	1,345	306	479
9/27-28/2010	935	186	396	20	42	100	36	30	35	2,100	1,294	257	548
9/27-28/2011	840	187	352	22	42	83	39	30	32	2,270	1,383	308	579
9/27,30/2012	940	224	383	24	41	85	33	28	39	2,350	1,429	340	581
9/28/2013[c]	184	33	78	18	42	136	29	38	32	2,300	1,435	257	608
9/28-29/2014	922	210	407	23	44	75	32	24	44	2,500	1,498	341	661
10/1/2015	781	189	368	24	47	58	34	30	36	2,780[d]	1,623[d]	393[d]	765[d]

[a] Cows ≥ 1 year old.

[b] S = small: antlers indistinguishable from those of adult cows, body size comparable to cows.
M= medium: antlers larger than adult cows, but having smaller beam diameter, fewer points, and/or shorter antler length than the large bull class.
L = large: antlers fully developed with large diameter beams, many points, and long antler length.

[c] Limited survey conducted only south of Alaska Range due to persistent inclement weather on northern ranges and the partial shutdown of the Federal government that began 1 October 2013.

[d] 2015 herd size estimate and composition are tentative.

Table 2. Estimated natality rates for the Denali Caribou Herd, Denali National Park and Preserve, Alaska during 1987-2015. Rates are based on calving season observations of a sample of radiocollared females $\geq$ 1 year old designed to approximate the age structure of the population.

Year	*n*	Pregnant	Not Pregnant	Natality Rate %	95% Cl
1987	37	26	11	70.3	53.0 - 84.1
1988	46	33	13	71.7	56.5 - 84.0
1989	55	37	18	67.3	53.3 - 79.3
1990	49	29	20	59.2	44.2 - 73.0
1991	44	29	15	65.9	50.1 - 79.5
1992	46	41	5	89.1	76.4 - 96.4
1993	41	27	14	65.9	49.4 - 79.9
1994	47	43	4	91.5	79.6 - 97-6
1995	50	43	7	86.0	73.3 - 94.2
1996	53	46	7	86.8	74.7 - 94.5
1997	53	42	11	79.3	65.9 - 89.2
1998	46	39	7	84.8	71.1 - 93.7
1999	48	43	5	89.6	77.3 - 96.5
2000	55	46	9	84.6	71.2 - 92.2
2001	52	43	9	82.7	69.7 - 91.8
2002	45	38	7	84.4	70.5 - 93.5
2003	42	31	10	73.8	58.0 - 86.1
2004	53	45	8	84.9	72.4 - 93.3
2005	57	43	14	75.4	62.2 - 85.9
2006	62	44	18	71.0	58.1 - 81.8
2007	65	47	18	72.3	59.8 - 82.7
2008	68	53	15	77.9	66.2 - 87.1
2009	71	52	19	73.2	61.4 - 83.1
2010	66	49	17	74.2	62.0 - 84.2
2011	63	53	9	85.5	74.2 - 93.1
2012	65	52	13	80.0	68.2 - 88.9
2013	66	53	13	80.3	68.3 - 88.7
2014	66	49	17	74.2	61.8 - 83.9
2015	72	55	17	76.4	64.7 - 85.3

Table 3. Results of post-calving composition surveys of the Denali Caribou Herd, Alaska, 1984-2015.

Date	Cows > 1 YO	Calves	Calf:Cow Ratio
5/30-31,6/3/1984	519	201	39:100
1985		NO SURVEY	
5/28/1986	335	134	40:100
5/29-30/1987	1,124	487	43:100
5/27-29/1988	1,002	435	43:100
5/30/1989	1,263	500	40:100
6/1/1990	1,402	512	37:100
6/4-5/1991	1,213	220	18:100
6/1/1992	909	278	31:100
6/2-3/1993	822	177	22:100
6/1-2/1994	985	376	38:100
5/30/1995	693	238	34:100
5/29/1996	682	139	20:100
5/31/1997	759	101	13:100
5/29-30/1998	624	141	23:100
5/29/1999	522	108	21:100
6/7/2000	665	68	10:100
6/6/2001	736	140	19:100
6/8/2002	431	120	28:100
6/8/2003	613	104	17:100
6/6/2004	673	236	35:100
6/8-9/2005	798	193	24:100
6/9,11/2006	576	218	38:100
6/8-9/2007	953	321	34:100
6/7-9/2008	910	275	30:100
6/7-8/2009	1,036	359	35:100
6/9-10/2010	1,038	316	30:100
6/8-9/2011	1,141	377	33:100
6/15/2012	702	260	37:100
6/14-15/2013	981	325	33:100
6/14-15/2014	1,060	297	28:100
6/13-14/2015	1,236	481	39:100

Fig. 1. Population estimates for the Denali Caribou Herd, Denali National Park, Alaska, late September, 1986-2015 (2015 estimate is preliminary).

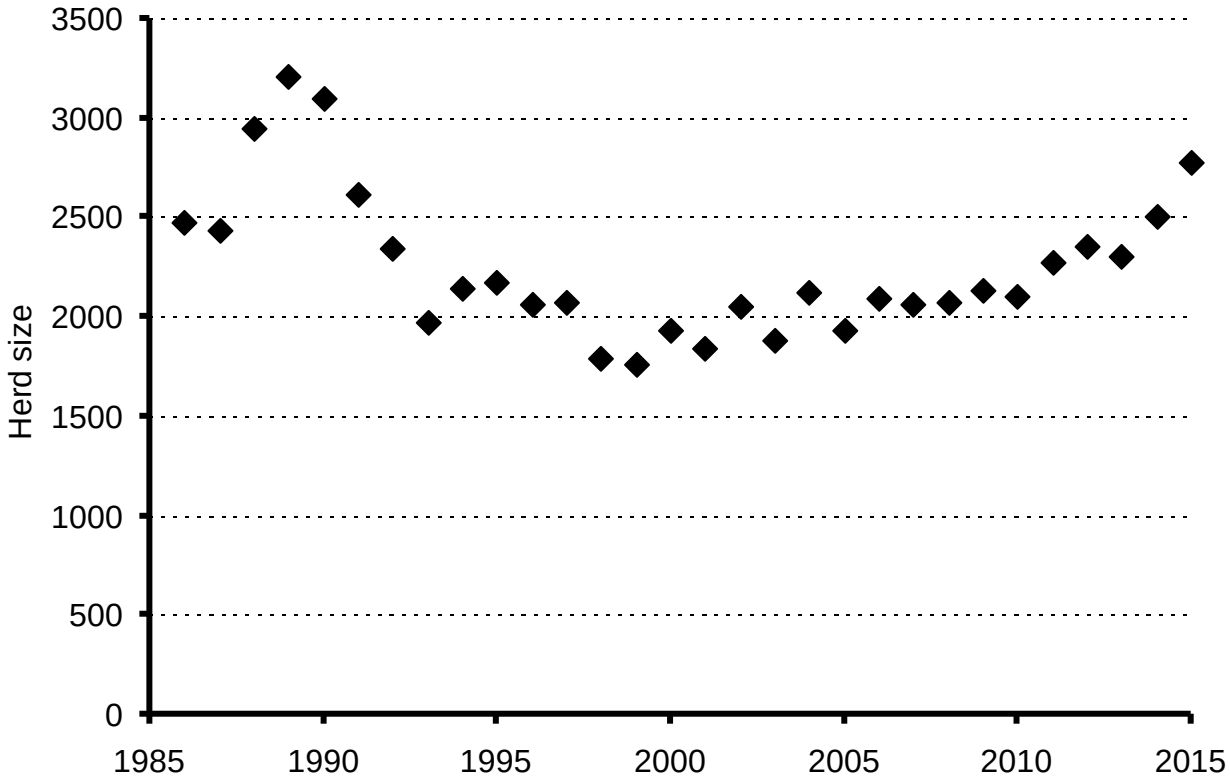


Fig. 2. Calf:cow ratios (A) and bull:cow ratios (B) for the Denali Caribou Herd, Denali National Park, Alaska, late September, 1984-2015.

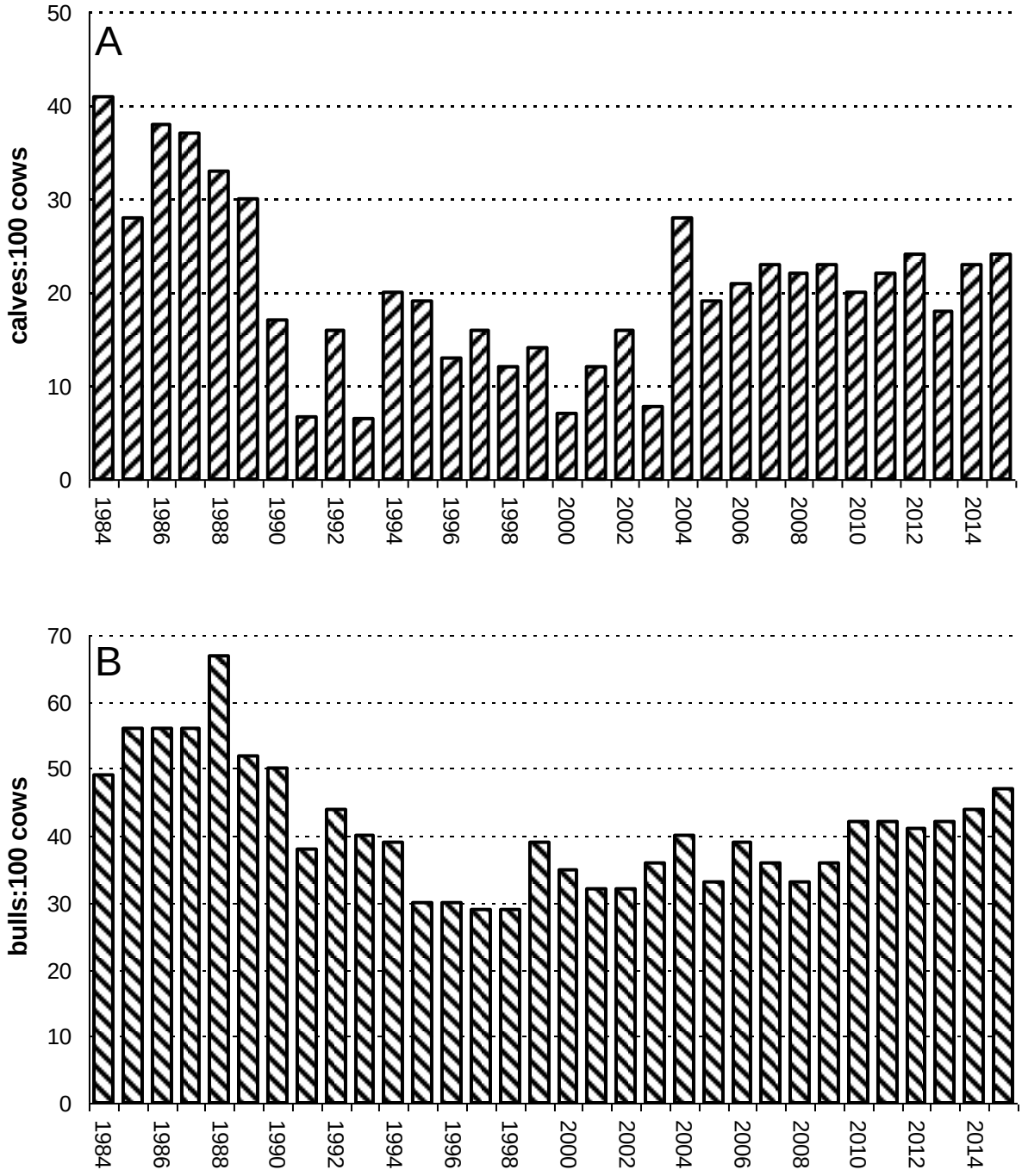


Fig. 3. Estimated calf survival to late September in the Denali Caribou Herd during 1987 – 2015, based on annual estimates of natality of radiocollared cows, adult female survival, and fall calf:cow ratios.

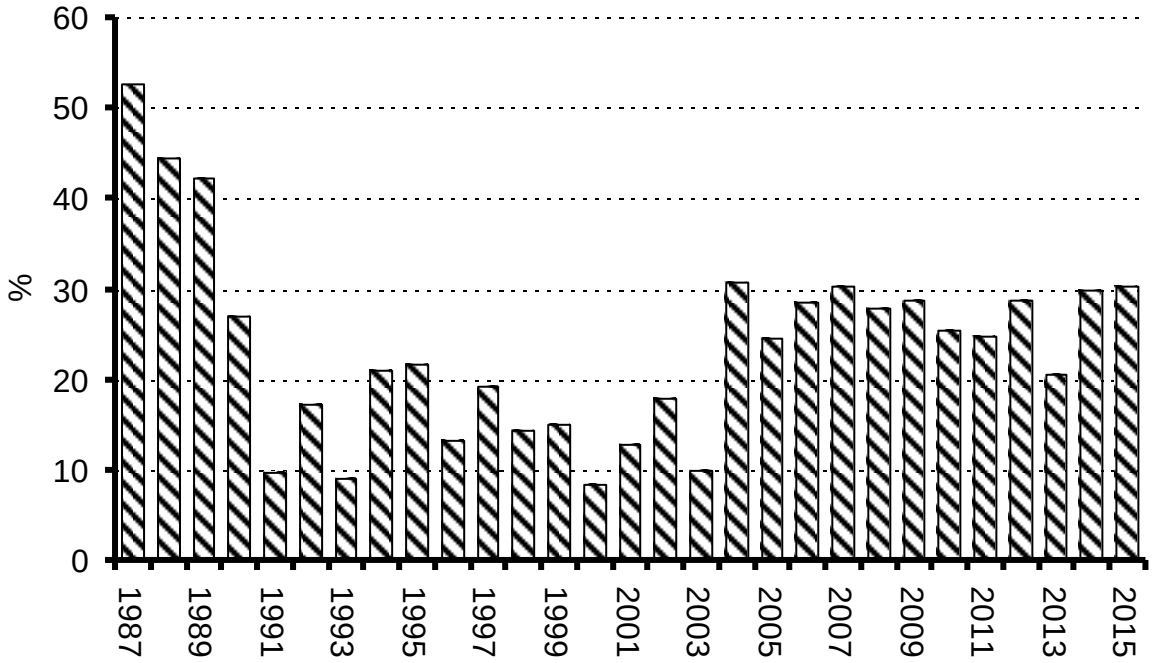


Fig. 4. Estimated age structure of the female segment of the Denali Caribou Herd on 1 May 2015 (*n* = 72 cows).

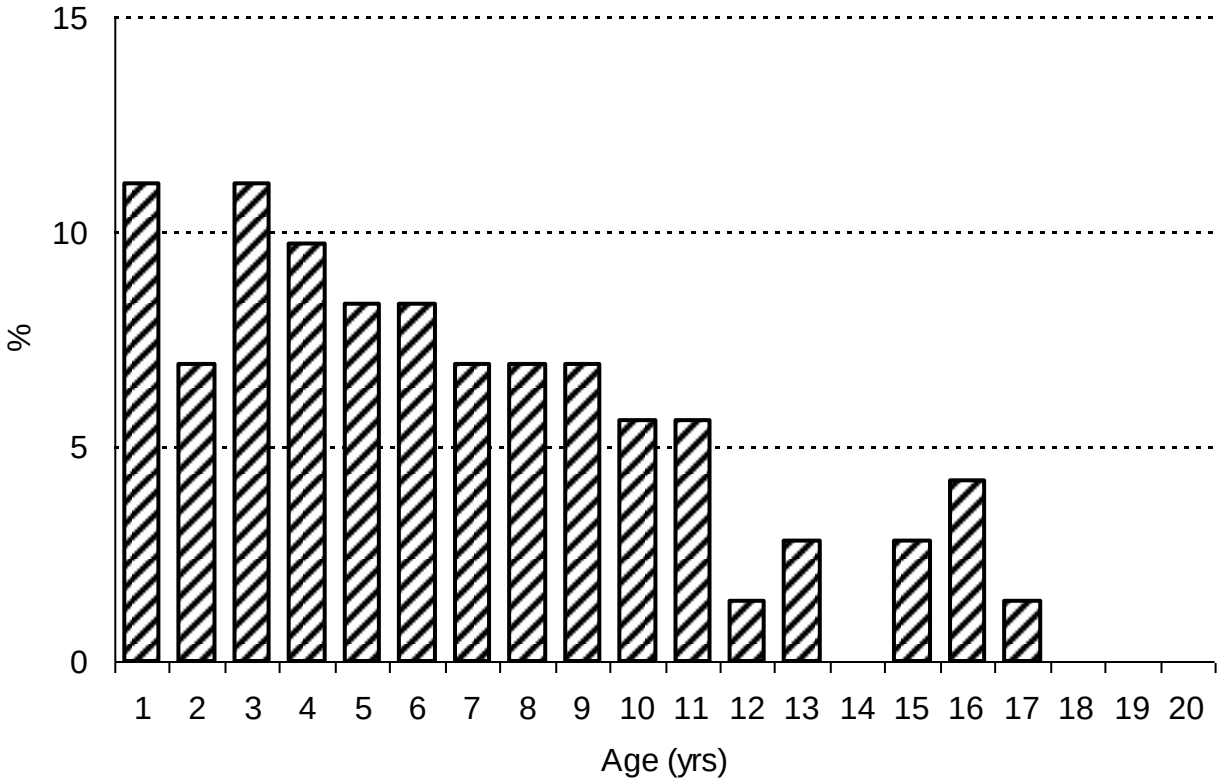


Fig. 5. Proportion of the adult female segment of the Denali Caribou Herd ≥ 13 years old on 1 May 1987-2015.

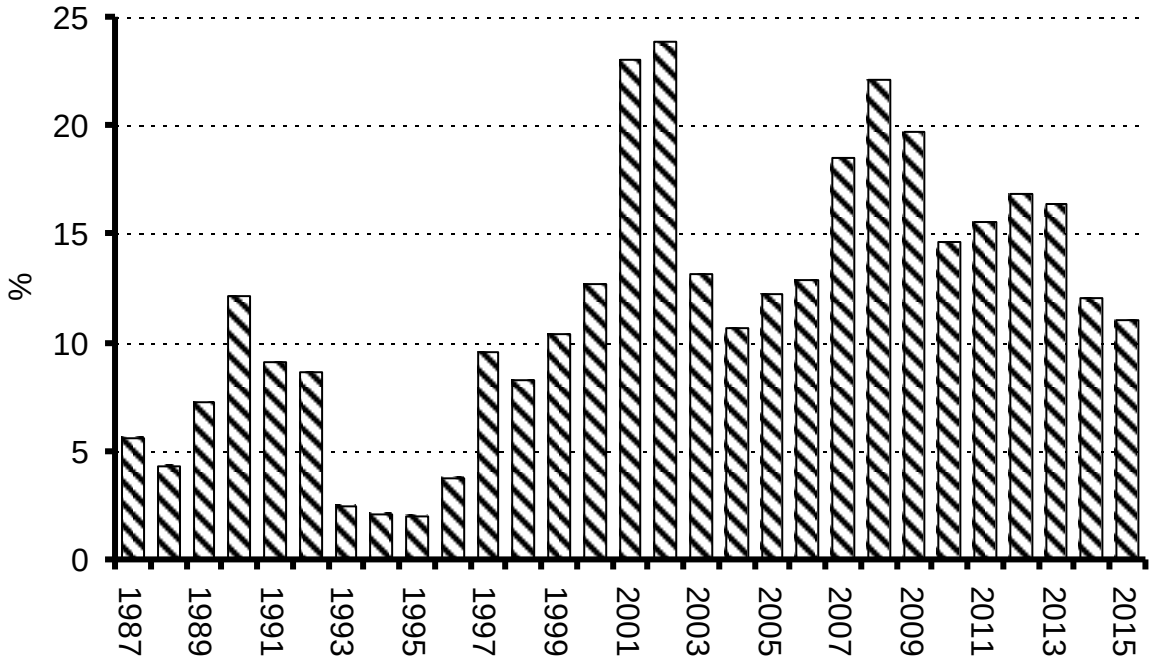


Fig. 6. Age-specific survival rates (± 95% confidence intervals) for female Denali caribou, based on 394 individual caribou monitored for 1,955 caribou years during October 1986-September 2013.

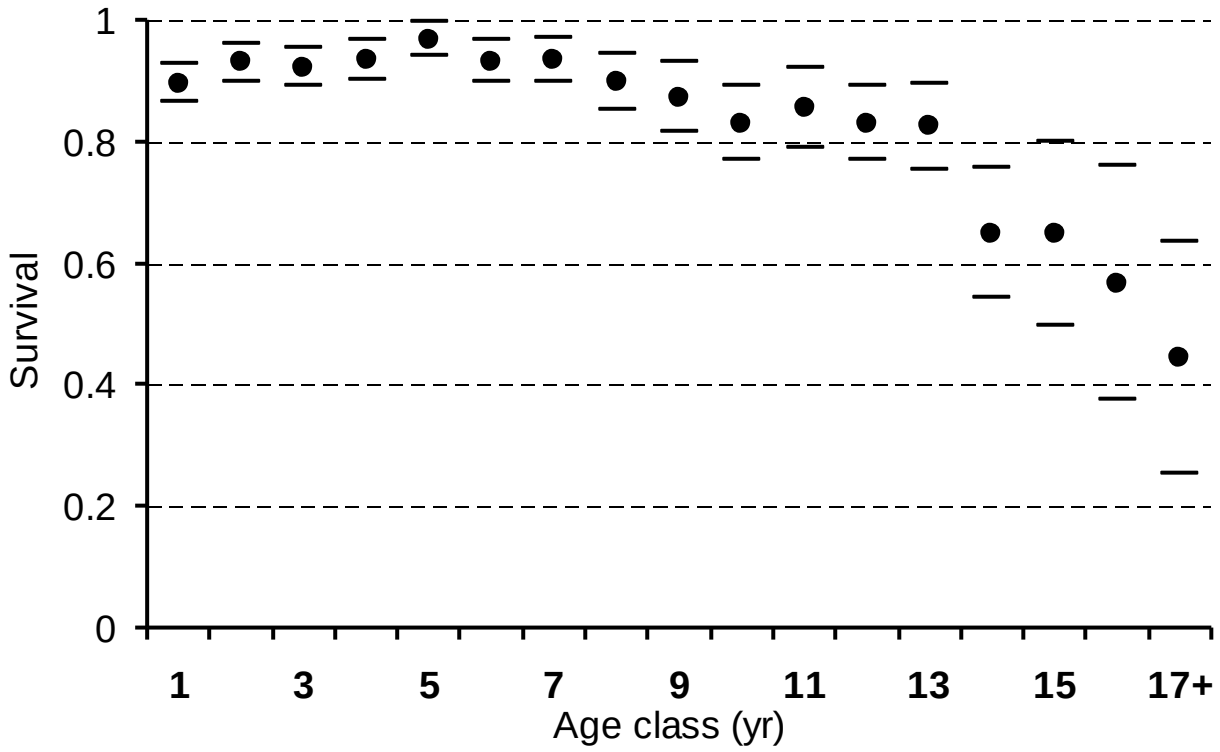


Fig. 7. Body masses of bull caribou ≥ 1 year old (*n* =195) weighed in September 2007-2015. Dashes indicate means for age-classes including ≥ 4 individuals.

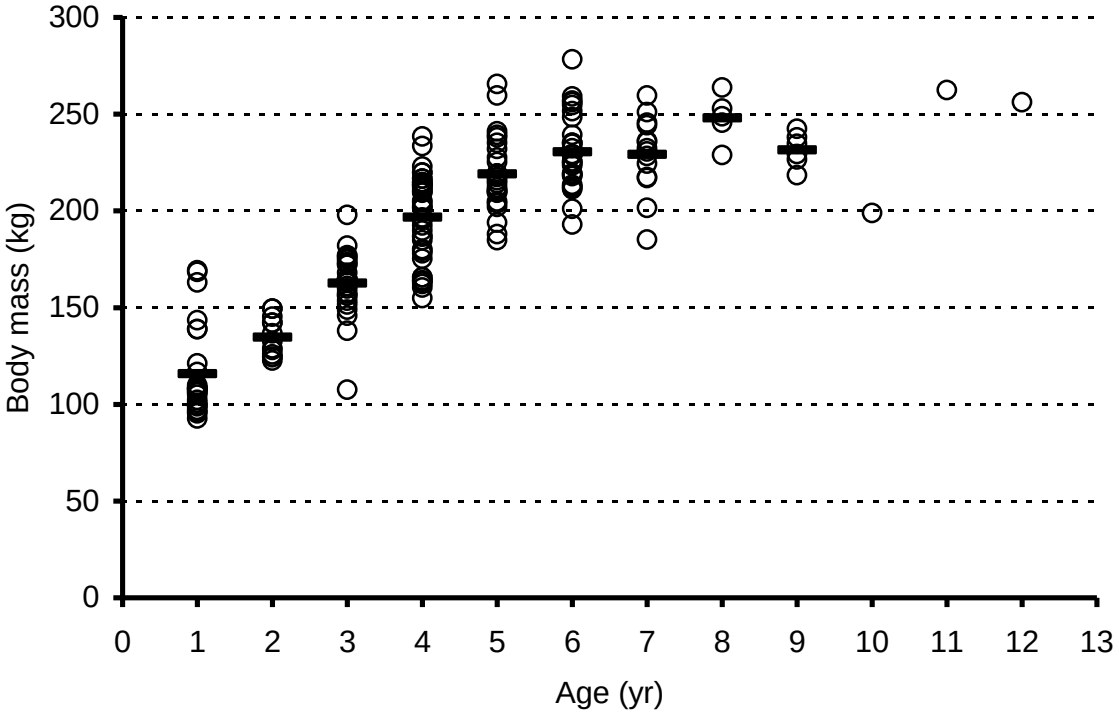


Fig. 8. Estimated survival rates (± 95% confidence limits) by age-class for male caribou in the Denali Herd, based on 198 individual caribou monitored for 488 caribou years during October 2007 –September 2015.

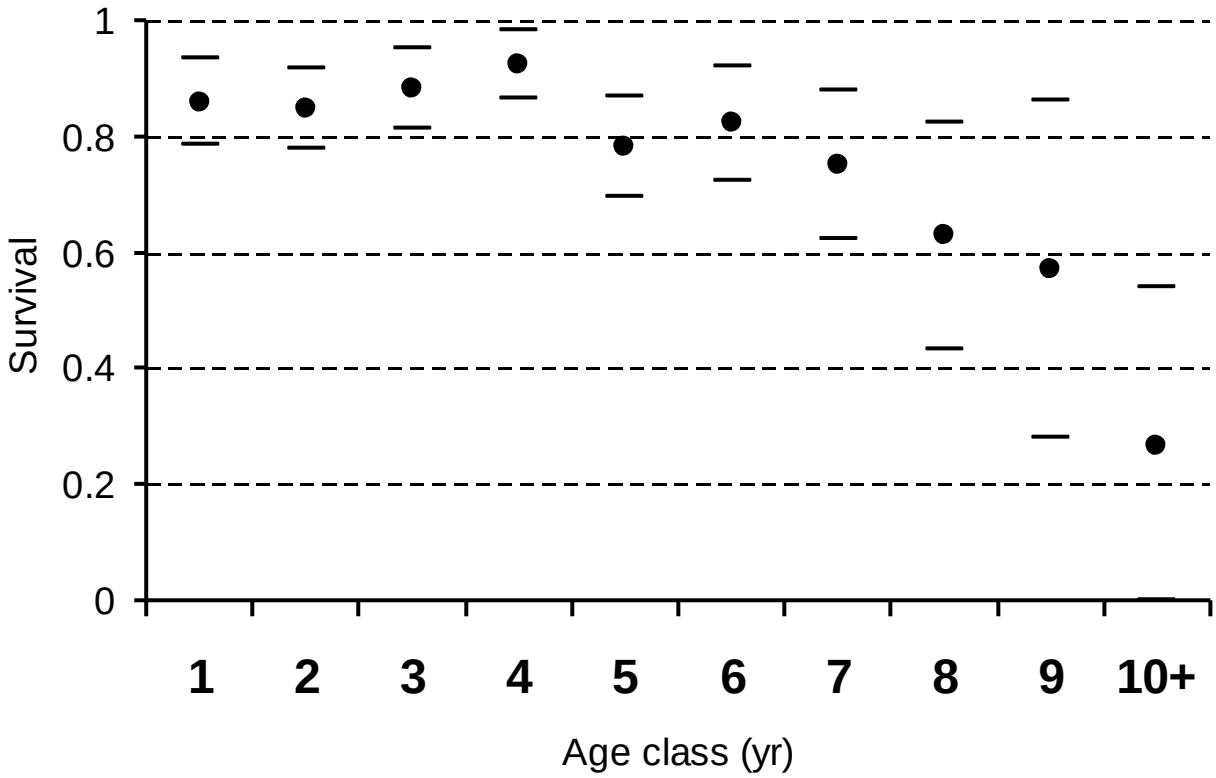
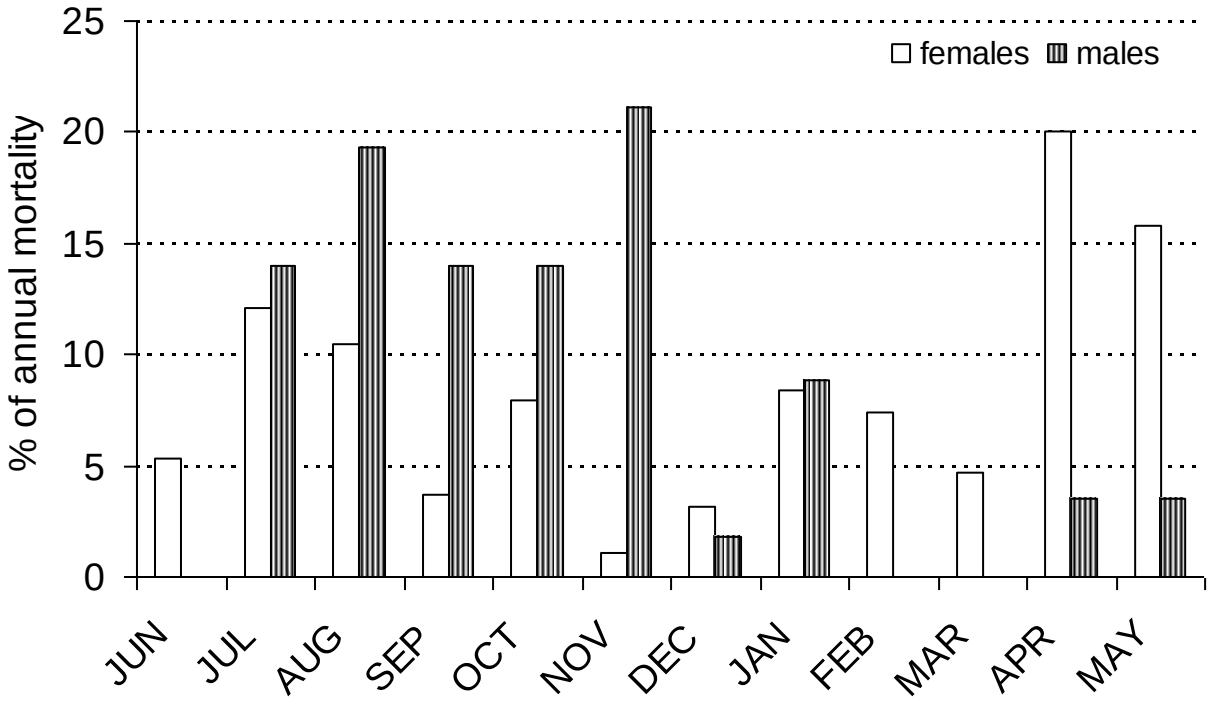


Fig. 9. Timing of annual mortality for male and female caribou ≥ 5 years old in the Denali Herd, based on radiotelemetry data collected during October 1986-September 2013 for females (*n* = 190 deaths), and October 2007-September 2015 for males (*n* = 57 deaths).



Appendix 1. Products of the Denali Caribou research program during 1986-2015.

Report – Adams, L.G. 2015. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2013 – September 2014). USGS Alaska Science Center, Anchorage, AK. 25pp.

Report – Adams, L.G. 2014. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2012 – September 2013). USGS Alaska Science Center, Anchorage, AK. 26pp.

Report – Adams, L.G. 2013. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2011 – September 2012). USGS Alaska Science Center, Anchorage, AK. 24pp.

Report – Adams, L.G. 2012. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2010 – September 2011). USGS Alaska Science Center, Anchorage, AK. 29pp.

Publication -Gustine, D.D., P.S. Barboza, J.P. Lawler, L.G. Adams, K.L. Parker, S.M. Arthur, and B.S. Shults. 2012. Diversity of nitrogen isotopes and correlates of protein balance in caribou: implications for monitoring northern ungulates. Journal of Mammalogy 93:778-790.

Report – Adams, L.G. 2011. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2009 – September 2010). USGS Alaska Science Center, Anchorage, AK. 24pp.

Report – Adams, L.G., and G.H. Roffler. 2010. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2008 – September 2009). USGS Alaska Science Center, Anchorage, AK. 35pp.

Report – Adams, L.G., and G.H. Roffler. 2009. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2007 – September 2008). USGS Alaska Science Center, Anchorage, AK. 18pp.

Report – Adams, L.G., and G.H. Roffler. 2008. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2006 – September 2007). USGS Alaska Science Center, Anchorage, AK. 20pp.

Report – Adams, L.G., and G.H. Roffler. 2007. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2005 – September 2006). USGS Alaska Science Center, Anchorage, AK. 17pp.

Publication - Adams, L.G., T. Meier, P. Owen, and G.H. Roffler. 2006. Interrelationships of Denali's large mammal community. Alaska Park Science 5(1):36-40.

Report – Adams, L.G., and G.H. Roffler. 2006. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2004 – September 2005). USGS Alaska Science Center, Anchorage, AK. 15pp.

Publication - Adams, L.G., B.W. Dale, and G.H. Roffler. 2005. Extraordinary movements of the Denali Caribou Herd following the perfect storm. Rangifer Special Issue 16:19-25.

Publication - Adams. L.G. 2005. Effects of maternal characteristics and environmental variation on birth masses of Alaskan caribou. Journal of Mammalogy 86:506-513.

Report – Adams, L.G. 2005. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2003 – September 2004). USGS Alaska Science Center, Anchorage, AK. 16pp.

Report – Adams, L.G. 2004. Dynamics of the Denali Caribou Herd, Denali National Park, Alaska: progress report (October 2002 – September 2003). USGS Alaska Science Center, Anchorage, AK. 11pp.

Publication - Adams, L.G. 2003.Marrow fat deposition and skeletal growth in caribou calves. Journal of Wildlife Management 67:20-24.

Report - Adams, L.G. 2002. Population dynamics of wolves and their prey in Denali National Park, Alaska: progress report (May 2000 - April 2001). USGS Alaska Biological Science Center, Anchorage, AK. 26pp. + appendices.

Publication - Ben-David, M., E. Shochat, and L.G. Adams. 2001. The utility of stable isotope analysis in studying foraging ecology of herbivores: examples from moose and caribou. Alces 37:421-434.

Report - Adams, L.G. 2001. Population dynamics of wolves and their prey in Denali National Park, Alaska: progress report (May 1998 - April 2000). USGS Alaska Biological Science Center, Anchorage, AK. 26pp. + appendices.

Report - Adams, L.G. 1999. Population dynamics of wolves and their prey in Denali National Park, Alaska: progress report. USGS Alaska Biological Science Center, Anchorage, AK. 17pp. + appendices.

Publication - Adams, L.G., and B.W. Dale. 1998. Reproductive performance of female Alaskan caribou. Journal of Wildlife Management 62:1184-1195.

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Publication - Adams, L.G., F.J. Singer, and B.W. Dale. 1995. Caribou calf mortality in Denali National Park, Alaska. Journal of Wildlife Management 59(3):584-594.

Publication - Adams, L.G., B.W. Dale, and L.D. Mech. 1995. Wolf predation on caribou calves in Denali National Park, Alaska. Pages 245-260 in L.N. Carbyn, S.H. Fritts, and D.R. Seip, eds. Ecology and conservation of wolves in a changing world - proceedings of the second North American symposium on wolves. Canadian Circumpolar Institute Occasional Paper 35. University of Alberta, Edmonton. 642pp.

Publication - Adams, L.G., and L.D. Mech. 1995. Population trends of wolves and caribou in Denali National Park, Alaska. Pages 347-348 in E.T. LaRoe, G.S. Farris, C.E. Puckett, P.D. Doran, and M.J. Mac, eds. Our living resources: a report to the nation on the distribution, abundance, and health of U.S. plants, animals and ecosystems. U.S. Department of Interior, National. Biological Service, Washington, DC. 530pp.

Popular article - Adams, L.G. 1992. Snowfall tips the balance of wolf-caribou relationships in Denali National Park. Pages 56-57 in Highlights of natural resource management. U.S. Department of Interior, National Park Service, Washington, DC. 67pp.

Publication - Davis, J.L., L.G. Adams, P. Valkenburg, and D.J. Reed. 1991. The relationship between caribou body weight and age and cohort specific reproduction. Pages 115-142 in Butler, C.E. and S.P. Mahoney (eds.). Proceedings of the fourth North American caribou workshop. Newfoundland and Labrador Wildlife Division, St. John's, Newfoundland. 529pp.

Report - Adams, L.G., B.W. Dale, and B. Shults. 1989. Population status and calf mortality of the Denali Caribou Herd, Denali National Park and Preserve, Alaska - 1984-1988. U.S. National Park Service Natural Resources Progress Report AR-89/13. Anchorage, AK. 131pp.

Publication - Adams, L.G., B.W. Dale, and F.J. Singer. 1988. Neonatal mortality in the Denali Caribou Herd. Proceedings of the third North American caribou workshop. Alaska Department of Fish and Game Wildlife Technical Bulletin 8:33-34.

Publication - Adams, L.G., P. Valkenburg, and J.L. Davis. 1988. Efficacy of carfentanil citrate and naloxone for field immobilization of Alaskan caribou. Proceedings of the third North American caribou workshop. Alaska Department of Fish and Game Wildlife Technical Bulletin 8:167-168.

Popular article - Adams, L.G. 1987. Fate of caribou calves studied in Denali. Page 16 in Highlights of natural resource management. U.S. Department of Interior, National Park Service, Washington, DC. 53pp.

Report - Adams, L.G. 1986. Population status and neonatal mortality of the Denali Caribou Herd-progress report. U.S. National Park Service Natural Resources Progress Report AR-86/05. Anchorage, AK. 13pp.