RELATIONSHIPS BETWEEN BODY WEIGHT, EARLY PUBERTY, AND REPRODUCTIVE HISTORIES IN CENTRAL ALASKAN CARIBOU

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Abstract: Reproductive histories were determined for known-age radio-collared caribou (Rangifer tarandus granti) in the Delta Caribou Herd from 1979 to 1989. During this time, herd size grew from <4,000 to >10,000. Live weights were obtained in most years from 11-month-old females (as an index of cohort condition). No significant change in mean body weight of cohorts occurred over time, but the parturition rate of 24-month-old females dropped from 67% in 1980 to 0% after 1983. Corroborating data from the adjacent Denali Herd are included. Discussion focuses on the hypothesis that the main factor relating to pregnancy in caribou is female body weight at rut. In addition, we discuss (1) effect of early puberty on pregnancy resting and alternate-year reproduction, (2) pregnancy resting in non-early puberty females, and (3) conditions associated with and demographic consequences of early puberty in female caribou.

INTRODUCTION

When we began intensive research on the Delta Caribou Herd in the late 1970s, data were limited on the variables affecting reproduction in Alaska's caribou. Also, opinions were diverse regarding the relative importance of nutrition to caribou reproduction and hence population dynamics. For example, at a symposium and workshop on caribou population ecology in Alaska (Klein and White 1978:22-23), E. Reimers suggested that a close relationship exists between pregnancy rate and body weight of females at the time of rut. Based on Norwegian data, where predators were unimportant sources of mortality to caribou, Reimers concluded that, "...herd productivity was highly dependent on individual animal growth."

In contrast, A. T. Bergerud (Klein and White 1978:23) stressed that reproductive rates in North American caribou herds remain relatively constant at 70-85% despite a wide diversity in range conditions. Also, he stressed that the major influences on caribou numbers, and in particular what brings their numbers down, are predator-prey interactions.

Lacking specific knowledge of the variables affecting reproduction in North America, there has been a tendency to extrapolate from the Scandinavian literature on domestic and wild reindeer (e.g., R. G. White, pers. commun.; Klein and White 1978:37) with considerable emphasis on Reimers' (1983a,b) work.

Also, lacking empirical data from females of known reproductive histories and sequential annual weights at rut, several popular hypotheses have emerged and gone untested for a decade or more. Examples include Reimers' (1983a) hypothesis that from the weight distribution of females in a population the population's pregnancy rate can be calculated by the following equation: $P = 1 - e\,[-0.169\,(W-21)]$, where P = probability of pregnancy, and W = dressed weight in kg (dressed weight = total body weight minus viscera, head, skin, and lower legs).

A second hypothesis is that repeated pregnancy and lactation will thus eventually result in a "pregnancy resting" year (Dauphine 1976, Reimers 1983a). A third hypothesis is that early puberty could result in a developmental setback, leading to a temporary barren status the next breeding season (Reimers 1983a), or 2 seasons (Lenvik 1981 cited in Reimers 1983a), or even to a pattern of alternate-year reproduction (R. G. White, pers. commun.).

In addition, interest remains high in the management implications of early puberty in caribou herds. Early breeding can potentially contribute greatly to herd growth because young-age cohorts are relatively large in populations with a "normal" age structure (i.e., stable or increasing herds). However, the actual contribution depends on survivorship of the offspring and whether producing a calf at 2 years of age will cause the female to "pregnancy rest" in some subsequent year or years.

Radio-collaring of Delta caribou females <12 months old began in 1979. The primary objective of the radio-collaring was to ascertain age-specific mortality and reproduction. In addition, the project allowed us to collect serial whole body weights and total reproductive histories of individuals. Similar work began on the adjacent Denali Caribou Herd in 1986. We believe that the data from the Delta and Denali studies can be used to evaluate the hypotheses stated above and/or as evidence for alternate hypotheses.

OBJECTIVES

1. To test the hypothesis that pregnancy rates are related predictably to body weights of females (Reimers 1983a).
2. To ascertain if early puberty increased the probability of alternate year reproduction or "pregnancy resting" at 3 years of age in Delta caribou.
3. To review and discuss the evidence for pregnancy resting in caribou.
4. To identify the conditions associated with early puberty in the Delta and Denali Herds and to evaluate the demographic consequences of early puberty in the population dynamics of caribou herds.

STUDY HERDS AND AREAS

The Delta and Yanert Caribou Herds currently range over about 11,000 km^2 on the north slopes of the Alaska Mountain Range between the Nenana River on the west and the Delta River on the east and seasonally overlap in distribution (Fig. 1). The Denali Herd inhabits an area of approximately 10,000 km^2 adjacent to the Delta and Yanert Herds, bounded by the Nenana River on the east and the Herron River on the west. The area inhabited by these herds lies approximately 110 km south of Fairbanks. The Alaska Range consists of rugged, glaciated ridges, 1,830-2,740 m in elevation, interspersed with glacier-capped mountains exceeding 3,660 m. The northern foothills of the Alaska Range are flattopped ridges, 610-1,370 m in elevation, separated by rolling tussock tundra, muskegs, and lowlands dominated by spruce (<u>Picea</u> spp.) North of the foothills lies the predominantly spruce-covered Tanana Flats. The entire area is drained by the Tanana River.

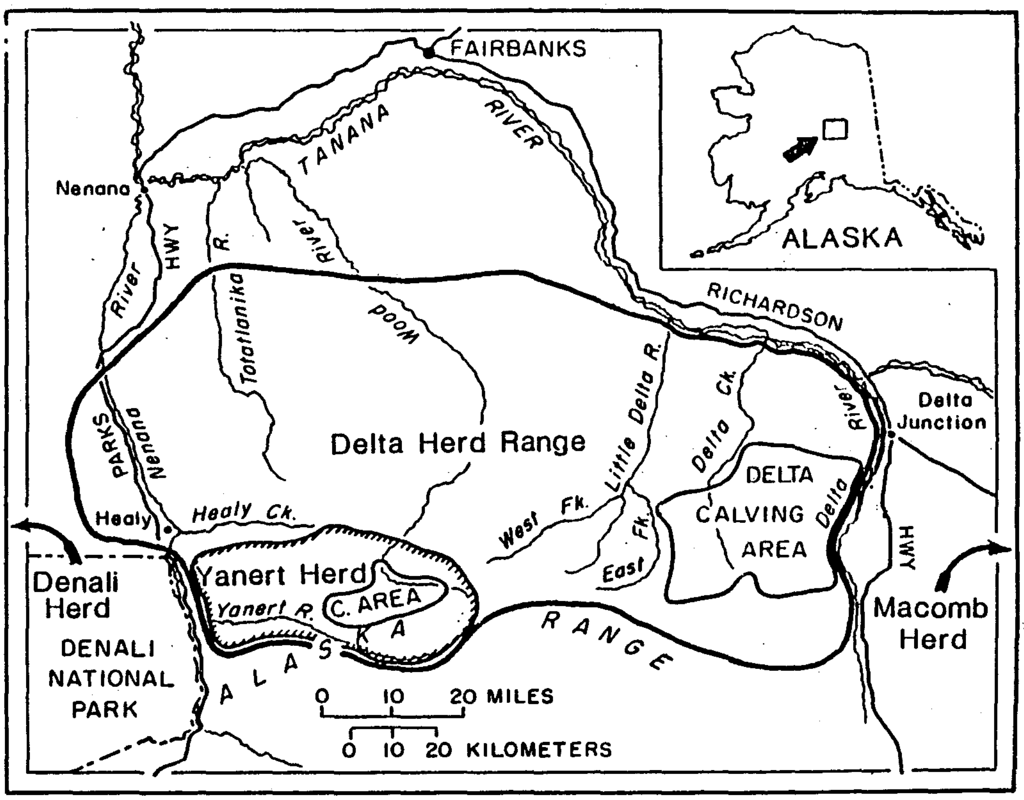

Fig. 1. The delta and Denali study areas.

The area is largely snow-free from May until October. Annual temperature range is approximately 29°C to -51°C. Annual precipitation averages about 30 cm; snow accumulation averages 50 cm and rarely exceeds 80 cm. In the foothills and mountains, ground vegetation is frequently exposed during winter by strong winds.

Large predators in the study areas include wolves (Canis lupus), black bears (Ursus americanus), and grizzly bears (Ursus arctos). Additional predators capable of preying on caribou include coyotes (Canis latrans), wolverines (Gulo gulo), Lynx (Lynx canadensis), golden eagles (Aquila chrysaetos), and possibly red fox (Vulpes fulva). Major prey species present include moose (Alces alces), caribou, Dall sheep (Ovis dalli), beavers (Castor canadensis), snowshoe hares (Lepus americanus), and ground squirrels (Citellus parryi). Population status and history of the Delta and Yanert Herds was last reported by Davis et al. (1988). During the past 2 decades, the Delta Caribou Herd has varied dramatically in size and population density, declining from 5,000 ($0.6/km^2$) in 1969 to about 2,000 ($0.31/km^2$) in 1975 and increasing from about 2,000 in 1975 to 7,000 ($0.8/km^2$) in 1982. Since 1982, herd growth has been slowed by hunting (and perhaps other factors) reaching >10,000 ($1.0/km^2$) in July 1989. The Yanert Herd was first recognized as a discrete herd in 1980 and has apparently numbered 600+/-200 since then but has become seasonally overlapped in distribution by the Delta Herd.

Davis et al. (1983) surmised that nutritional status was high in the

Delta Herd based on nutritional indices such as rapid growth, large body size, early sexual maturity, high pregnancy rates, high natality and calf survival rates, and early parturition. Because the Delta and Yanert Herds have shared seasonal ranges since 1984, we believe that nutritional status is similar for the 2 herds, so data are pooled in this paper and hereafter referred to as Delta Herd data.

The population status and history of the Denali Herd has been reported by Boertje (1981), Singer (1987), and Adams et al. (1989). The herd numbered around 1,000 animals in the mid-1970s after a major decline from about 9,000 animals in the early 1960s. Historically, the Denali Herd may have numbered over 20,000 in the late 1930s-early 1940s. Boertje (1981) characterized the herd during the early 1980s as a reduced population with high nutritional status and a population density of around 0.08 to 0.12 caribou per km^2. Recent work by Adams et al. (1989) suggests that the population grew to over 3,000 animals by 1989 (0.3 caribou/km2) and apparently has continued high nutritional status.

METHODS

Delta Caribou Herd

From January 1979 through April 1989, we captured and radio-collared 85 different female caribou from the Delta Herd. These females were collared primarily at 8-12 months of age. Collars were replaced every 3-4 years prior to battery exhaustion in the radio transmitters. Most caribou were immobilized by darting with M99 (Valkenburg et al. 1983) or Wildnil (Adams et al. 1988b) from a helicopter. The remaining caribou were captured with a shoulder-held net gun (Valkenburg et al. 1983) or a net gun mounted on the skids of a helicopter and handled without chemical immobilization or sedation. Age of radio-collared caribou was based on the presence of deciduous incisiform teeth for calves; older caribou were aged by cementum annuli (Miller 1974).

Davis et al. (1986) and Valkenburg et al. (1988) described the methods used to relocate caribou during the calving periods. We relocated caribou using Piper Super Cub or Bellanca Scout aircraft with J. Davis and/or P. Valkenburg as observer in all relocations. Each female >24 months old was located and observed a minimum of 1-3 times per calving season. For about 80% of the relocations, reproductive status was judged from the presence or absence of a distended udder (Bergerud 1964); in most remaining instances a calf was present and appeared bonded to the female. Occasionally, the presence of hard antlers in addition to subjective impressions by the observers was the basis for judging the female's parturition status. In 4 of 294 cases (all in 24-month-old caribou), we were unable to judge reproductive status.

Denali Caribou Herd

During March 1987 and 1988, 24 10-month-old female caribou were captured and radio-collared. All caribou were immobilized by darting with Wildnil (Adams et al. 1988b) from a helicopter.

During the years that they became >2 years old, all instrumented animals were relocated daily during 6-31 May until reproductive status could be determined. Cows that were believed to be pregnant were located daily until their calves were born. The calved were captured and radio-collared within 2 days of birth (Adams et al. 1988a, and 1989). Radio-collared calves were located daily until the end of May and then periodically throughout the rest of their first year.

Weight Conversions

We used Reimers' (1983b) conversion formula of dressed weight = 52% of the total body weight, to convert total body weights to dressed weights for calculations involving Reimers' (1983a) prediction equation: $P = 1 - e\ [-0.169(W-21)]$, where P = probability of pregnancy and W = dressed weight in kg.

Weights

In our testing of hypotheses about the relationship of rutting weight of females and their probability of being pregnant we used an index to rutting weight. Most of our weights were obtained around late April, so we must infer (perhaps invalidly?) a rut weight from those data. In doing so, we are assuming that significant between-year change in variables affecting weight gain over summer will be manifested in weights of that year's calf cohort when weighed in late winter. For example, we infer that if the x - weight of females from the 1978 cohort was 62 kg and if the x - weight of the 1979 and 1980 cohorts is also 62 kg, then the x - rutting weight at 17 months should be the same for the 1978 and 1979 cohorts. A corollary inference is that the within-cohort weight variation in year 1 will be proportionally the same in year 2.

RESULTS AND DISCUSSION

Objective 1: Body Weight - Pregnancy Relationships

Reimers (1983a) reviewed and summarized the literature regarding the main factors that relate to pregnancy in *Rangifer* as follows:

> "Skunke (1969) suggested that pregnancy rates relate to stocking rates and Movinkel and Prest-bakmo (1969) indicate a dressed weight relationship in domestic reindeer. Varo (1964, 1976), also working with domestic reindeer, found that pregnancy rate correlated to both age and weight. Skoog (1968), Kelsall (1968), and Parker (1982) found an age-dependent pregnancy rate in caribou. Dauphine (1976), although reporting an age-dependent pregnancy rate in caribou, found that pregnancy was clearly related to body weight and fat content .... Thomas (1982) shows that fertility in Peary caribou (*Rangifer tarandus pearii*) is related to the fat reserves."

Reimers (1983a) went on to conclude that reproduction data from wild and domestic reindeer in Norway indicate that pregnancy rates are related <u>Predictably</u> to body weights of the females. Reimers (1983b) amplified the view from his 1983a paper as follows:

> "Recently Hamilton and Blaxter (1980) for red deer ... Lenvik (1981) for domestic reindeer, Thomas (1982) for Peary caribou ... and Reimers (1983) for wild reindeer, have found that reproduction in these species or subspecies is a function of weight rather than age. This means that the pregnancy status of a female may be predicted once her rutting weight is known. In wild reindeer, when a female dressed weight (W) increased from 25 to 30 kg, her probability (P) of being pregnant increases from 0.49 to 0.78 (i.e., 49% to 78%) according to the equation: $P = 1 - e\ [-0.169(W-21)]$ (Reimers 1983e). Therefore, from knowledge of the weight distribution of females in a population, its pregnancy rate may be calculated."

We believe that much "conventional wisdom" on the relationship between body weight and its influence on reproduction stems from Reimers (1983a,b), discussion in Klein and White (1978:31), and R. G. White (pers. commun.).

If Reimers' prediction equation applies universally, the implications are important and many. Although it is unclear whether Reimers meant for his equation to apply throughout <u>R</u>. <u>tarandus</u>, we applied it to body weight data from the Delta Herd. Predictions from the equation did not compare well with our field data (Table 1).

Table 1. Comparison of Delta Caribou Herd body weights and pregnancy rates with predictions based on Reimers' (1983a) equation.

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Age (years)	Weight in kg $\bar{x}$ live	$\bar{x}$ dressed	n	SD	Actual pregnancy rate	(n)	Reimers' predicted rate	Adjusted[a] predicted rate	(90% CI)
1	61.4	31.9	82	5.4	0.0	84	0.84	0.0	
2	75.8	39.4	4	15.5	0.15	65	0.90	0.22	(0.0-0.69)
≥3	112.5	58.5	46	10.4	0.89	253	1.00	0.88	(0.86-0.88)

[a] An adjustment factor was calculated from the $\bar{x}$ weight of ≥3-year-old cows from this study (58.5 kg) and Reimers (1983a) (33.4 kg) as follows: 33.4/58.5 = 0.57. See text.

However, Reimers' original data (1983a:213, Table 2) resulted in an estimated pregnancy rate of 0.88 for reindeer ≥3 years old at the time of calving, the same as our observed rate for Delta caribou in that age group (Fig. 2). The mean dressed weight of Reimers' reindeer in this age category was 33.4 kg or 0.57 that of Delta caribou. When the 0.57 correction factor was applied to mean dressed weights for Delta caribou that were 1 or 2 years old at calving, the subsequent predicted pregnancy rates were 0.0 and 0.22, respectively, which generally agrees with field data. Therefore, Reimers' (1983a) prediction equation may apply for other than Norwegian reindeer, if a "correction factor" is applied to account for herd-specific differences in Rangifer body weights. Additional herd-specific and time-specific correction factors may be required to consider genetic effects, phenotype ratios, and environmental variables.

Table 2. Weight-related statistics for 7- to 12-month-old female caribou from Alaska's Delta Caribou Herd by cohort year.

Cohort year	Sample size	$\bar{x}$	SD	Minimum	Maximum
1978	11	61.3	3.7	58.8	63.7
1980	5	63.4	7.5	54.1	72.7
1981	11	62.4[a]	5.6	58.6	66.2
1982	14	64.8[a]	7.1	60.7	68.9
1983	12	58.6	2.2	57.1	60.0
1986	9	56.1[a]	3.8	53.2	59.0
1987	12	60.9	4.6	57.9	63.8
1988	9	61.9	3.7	59.0	64.7
Total	83	61.2[b]	5.4	60.0	62.4

[a] A Kruskal-Wallis non-parametric ANOVA and Student, Newman-Keuls multiple comparison on ranks test were combined to determine that the only significant (= 0.05) difference in cohort weights was that the 1981 and 1982 mean cohort weights were greater than in 1986.

[b] For comparison, $\bar{x}$ = 61.2 kg (n = 14) for 11-month-old females from the Denali Herd for the 1986 and 1987 cohorts combined.

While reviewing Reimers' (1983a, Table 2) original data, we arrived at 2 conclusions that differed from those of the author. First age may be an important influence on pregnancy rates. For the range of overlap in dressed weight (18-26 kg) between calves and older animals, 0 of 32 and 13 of 31, respectively, were pregnant. Hence, calves did not get pregnant regardless of body weight at the time of the rut. Parallel comparisons of yearlings and older reindeer over the range of overlap (27- 47 kg dressed weight) also indicated that yearlings had a lower probability of becoming pregnant (14 of 32) than did older reindeer (175 of 215) regardless of body weight. We suspect that age plays an important role, in addition to body weight, in determining pregnancy probabilities.

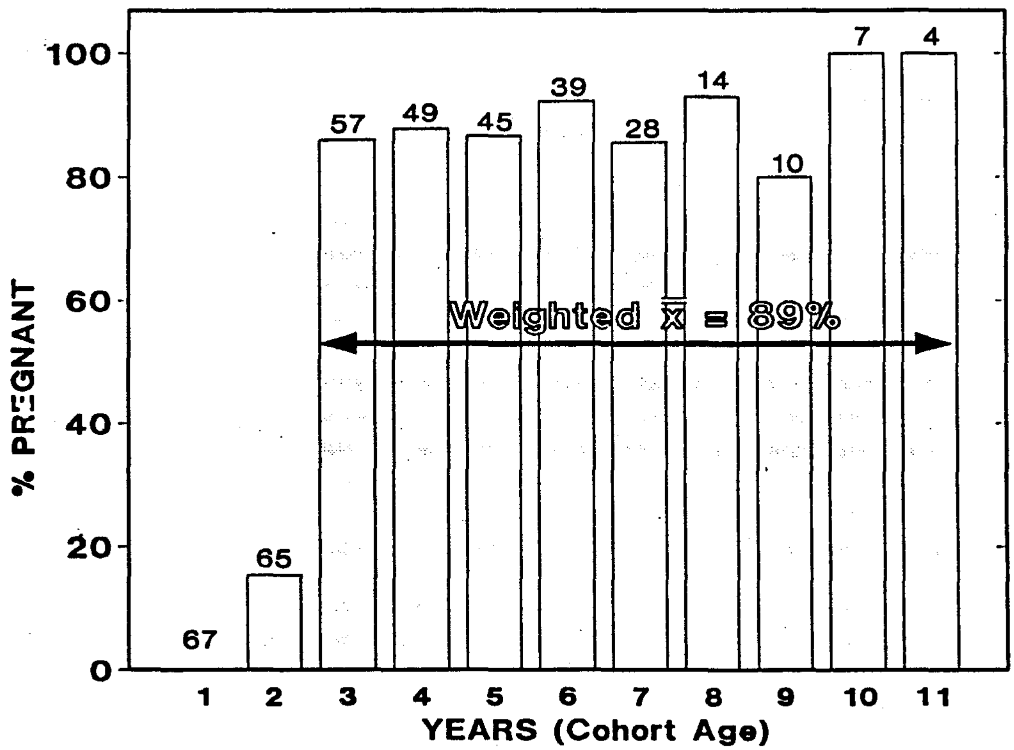

Fig. 2. Cohort specific pregnancy rates of known age Delta Herd caribou for ages 1-11 (sample size) 1979-1989.

Reimers (1983a) footnoted his Table 2 that only calves from Rondane, Hardangervidda, and Snohetta were weighed. He implied that calves from North and South Ottadalen were heavier. Reimers (1983b) reported that domestic reindeer have influenced both the North and South Ottadlen herds. "The domestic reindeer company ... discontinued its activity in 1964 .... Some animals were left behind in South Ottadalen and some (402 animals) were moved to North Ottadalen and given the status wild reindeer." So the variable of domestic vs. wild reindeer must also be considered if the argument is raised that the heavy calves from North and South Ottadalen might differently affect the data in Table 2. Bergerud (1980) commented as follows on the subject: "Jackson (1892-1908) suggests there has been some selection for early breeding in reindeer. Preobrazhenskii (1968) states that early breeding in reindeer fawns has a hereditary basis."

Also, we believe that the prediction of 100% pregnancy at 48+ kg carcass weight is less tenable than a model showing no significant difference in pregnancy rates above 30 kg carcass weight. Reimers' (1983a) own data indicate an 88% pregnancy rate for this weight range and provide no reason to believe that pregnancy rates reach 100% for heavy reindeer. Reimers (1983a) did report 100% pregnancy for small samples of the large-bodied North and South Ottadalen reindeer, but interpretation of these data, similarly to the case of calves, is confounded by influences of the domestic reindeer that founded these populations (i.e., possible selective breeding).

Although weight may often be a good index of reproductive condition for cervids, there are exceptions in the literature. Dusek et al. (1987) wrote as follows: "...body weight has been shown to be directly correlated with, and may be used to predict, reproductive rates in female whitetails (Sauer 1984) ... our recent analyses suggest that this traditional interpretation may need further qualification." Dusek et al. (1987) showed a higher reproductive level in a herd with smaller body weights than in a second herd with larger female body weights.

As food for thought, Geist (1983) commented that, "...in red deer size differences in extremes are five-fold (Beninde 1937)." We may have taken Geist's quote out of context, but this great size range implies great plasticity in pregnancy-weight relationships.

In summary, weight may reasonably predict pregnancy in some populations of _Rangifer_ (e.g., Reimers 1983a). However, we believe that one or more additional variables must be considered in conjunction with weight to create a predictor that might universally predict pregnancy probability in all _Rangifer_ populations.

Objective 2: Evaluation of Pregnancy Resting in Females First Reproducing at 24 Months of Age

Reproductive histories of females that first reproduced at 24 months of age appear in Fig. 3. We found no apparent pattern to indicate "pregnancy resting" at 36 months of age for these individuals. Only

1 of 8 females was nonparturient at 36 months of age resulting in an 88% parturition rate at 36 months for those females that reproduced at 24 months of age.

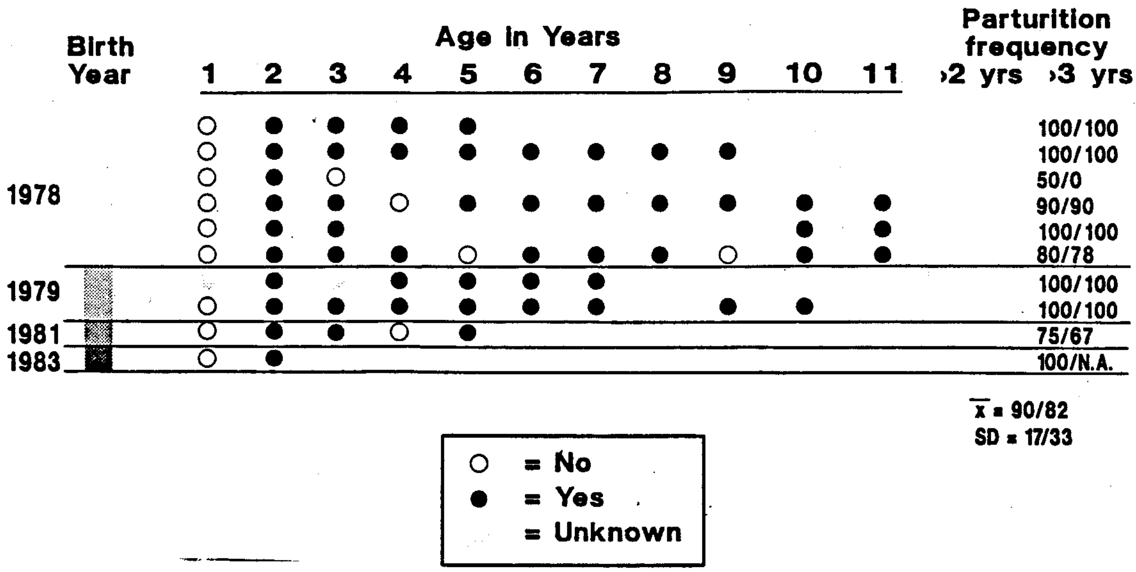

Fig. 3. Age-specific parturition status for 10 Delta Herd caribou that were first parturient at 24 months of age, 1978-89.

Of the 7 cows that were followed during each calving season at least to 5 years of age, 4 did not produce a calf in 1 of the 4 potentially productive years. There is no indication that "pregnancy resting" at 36 months or alternate year reproduction resulted from Delta caribou giving birth at 2 years of age. However, missed pregnancies did occur among some of these individuals between 3 and 5 years of age and the role of early puberty is unknown. Missed pregnancies following initial parturition occurred with comparable frequency among females that first gave birth at 3 years of age (Fig. 4).

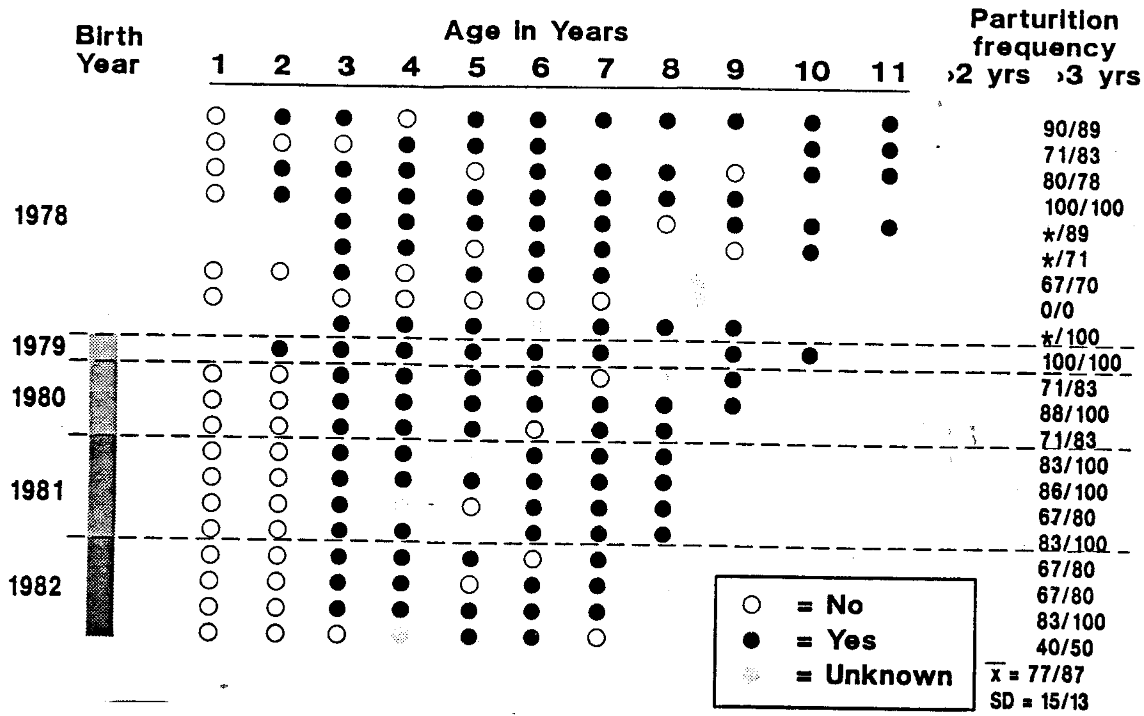

Fig. 4. Age-specific parturition status for 21 Delta Herd caribou with 6 or more years of known status, 1978-89.

<u>Objective 3: Evidence of Pregnancy Resting in Older Caribou</u>

The age-specific parturition records of 21 Delta caribou cows with 7 or more years of known status are summarized in Fig. 4. Cows that first calved when 3 years old were just as likely to have a calf the subsequent year (11 of 12, 92%) as were those that calved first at 2 years old (7 of 8, 88%).

Although the data in Fig. 4 do not provide a clear evaluation of "pregnancy resting" in the Delta Herd, it is unlikely that this phenomenon is important if lactation cost over the summer, rather than merely producing a calf, is the mechanism resulting in insufficient body condition to breed during the fall rut. In herds such as the Delta and Denali, early calf mortality is high resulting in few cows that support a calf through the summer.

The likelihood of having a calf survive in successive years is the annual calf survival rate exponentiated by the number of years. If calf survival to fall is only 0.5, then the likelihood of having a calf survive in 2, 3, or 4 successive years is 0.25, 0.13, and 0.06, respectively. If sequential successful calves are necessary to induce pregnancy resting, then in herds such as Delta and Denali it is unlikely to occur.

We did, however, detect considerable variation in parturition frequencies among individuals. For females >3 years old, the mean parturition rate was 87+/-13% and ranged from 0% to 100%. Even if pregnancy resting is important, individual variation may be so great as to mask its effects on productivity.

Working with bison (Bison bison), Lott and Galland (1985) employed known reproductive histories of individuals to test the hypothesis that a commonly observed reproductive rate was the result of each cow calving for 2 successive years, skipping a year, then repeating that 3-year cycle. Their records revealed large individual differences in fecundity and they concluded that the commonly observed reproductive rate could be alternatively explained by some cows calving several successive years while others calved rarely or never.

That fecundity can vary among individuals has important implications for modelers. For simplicity, many demographic and nutritional models implicitly assume that individuals within the model population are identical (i.e., clones). This assumption does not appear tenable given the huge and increasing evidence for polymorphism in practically all species, including caribou (Davis et al. 1986). It is entirely possible that fecundity could vary by phenotype (or genotype) partially independent of nutritional status. Alternatively, a large skeletoned individual (e.g., a dispersal phenotype <u>in</u> <u>insensu</u>, Geist (1983)) could weigh more than a (maintenance phenotype) smaller skeletoned individual in the same population, but be in poorer body condition which would confound using weight as an index to condition. Geist's (1983) dispersal and maintenance phenotypes present one mechanism by which the relative proportions of different phenotypes might occur in a given population over time.

<u>Objective 4: The Relationship Between Early Puberty and Demographic Variables in the Delta and Denali Herds</u>

Herds in the Delta Herd, the proportion of 24-month-old radio-collared females that were parturient varied as follows: 67% (8/12) for the 1978 and 1979 cohorts, 5% (2/37) for the 1980 through 1983 cohorts, and 0% (O of 17) for the post-1983 cohorts.

We did not determine any relationship between live weight at 7-12 months and the probability of being pregnant at 24 months of age.

The mean weight of all calves (7-12 months of age) that became pregnant at 24 months of age was $\underline{x}$ = 62.3 kg (n = 7, SD = 5.4) compared with $\underline{x}$ = 61.2 kg (n = 83, SD = 5.4) for all calves in the sample (Table 2). Further, in the highly parturient 1978 cohort, the $\underline{x}$ - weight of the cohort was 61.3 kg (n = 11, SD = 3.7); not significantly different from the entire sample mean (Table 2). The range of weights of the parturient females was 55.9 to 68.2 kg. Of nonparturient females, 30 equaled or exceeded the mean weight of parturient females of 62.3 kg. Also, 9 nonparturient females were heavier than the heaviest parturient female that weighed 68.2 kg.

Given that our data do not indicate a relationship between weight at 7- 12 months and the probability of being parturient in 24-month-old females, we decided to look for other variables present when early puberty was highest. We looked at the relationship between total population size, population density, and the relative abundance of adult males for the Denali (not in Table 3) and Delta Herds when the rate of early puberty was high and for the Delta Herd after the rate became 0 (Table 3). We also looked at wolf and grizzly bear:caribou ratios. Early puberty occurred in the Delta Herd at 67% frequency when the population density was $<0.5/km^2$; it occurred at 40% frequency in the Denali Herd at a density of $\leq 0.3/km^2$. Unfortunately, the quantity and quality of forage present was not quantified for the periods when early puberty occurred. Bergerud (1980) commented as follows regarding early puberty:

"With caribou the age of puberty varies little between years within established populations (Bergerud 1971, Dauphine 1976). However, when animals have been introduced into new ranges with longer growing seasons, invariably more yearlings reach puberty than on established ranges. Preobrazhenskii (1968) states that reindeer fawns reach puberty if there is good nutrition in autumn. These data suggest that nutrition during the first summer-of-life makes the main contribution to early puberty. Thus the growing season would be more important than the winter diet in attaining puberty."

Cohort year	Size of range km^2	Population size	% cohort parturition rate at 24 mos	Population density caribou:km^2	Wolf: caribou	Grizzly:[a] caribou	Bulls: 100 cows	Large[b] bulls: 100 cows
1978	8,023	3,200	67	0.40	1:84	1:26	75	NA
1979	8,023	3,831	67	0.48	1:101	1:31	39[c]	NA
1980	8,023	4,321	0	0.53	1:98	1:35	85	NA
1981	8,023	4,750	11	0.59	1:93	1:39	59	23
1982	8,023	6,545	0	0.83	1:111	1:53	54	24
1983	9,339	6,170	10	0.67	1:78	1:50	54	13
1984	10,007	5,660	NA	0.56	1:58	1:46	42	17
1985	10,339	7,483	0	0.71	1:63	1:61	49	9
1986	10,786	7,204	0	0.67	1:50	1:61	41	9
1987	10,786	7,780	0	0.71	1:47	1:61	32	8
1988	10,786	>8,000	NA	0.74	1:42	1:65	33	4
1989	10,786	10,000	NA	0.93	1:51	1:81	--	--

[a] Assumes 123 grizzlies in 1986 and ≥123 prior to 1986.
[b] Assumed to be ≥5 years old.
[c] Biased; real value probably about 75-80.

Table 3. Range size, population size, density, predator:caribou ratios, and bull:cow ratios of the Delta Caribou Herd, 1979-87.

Young age classes are significantly larger than older age classes in most stable or increasing caribou populations. The implication of this general rule is that early puberty can potentially influence herd productivity greatly. What role does early puberty play in irruptions of caribou populations? More specifically, what was the role in the irruption of the Delta Herd and in the current growth of the Denali Herd? What are the implications of early puberty to managers who want to maximize the number of caribou that can be produced annually from a caribou herd?

Reimers (1983a) reported that 2-year-old females constituted about 25% of all females 2 years old or older in his 5 study herds. Messier (1988) reported that 2-year-old females made up 21% of females >2 years old in a 1984 sample from the George River Herd which had been expanding.

An approximate parturition rate of 50% [the approximate mean of 67% (8/12) in the Delta Herd in 1978 and 1979 and 42% (10/24) in the Denali Herd in 1988 and 1989] appears to be a high rate for 24-month-olds in established North American herds (Bergerud 1980). A scenario involving a high rate of early puberty will allow assessing the contribution to total calf production added by early puberty. Assume 0.5 pregnancy in 2-year-olds, 0.9 pregnancy for >3-year-olds, and an age structure as in Messier (1988):

(0.79) (0.9) + (0.21) (0.5) = 0.71 + 0.11. Therefore, 82 calves/100 cows would be produced.

In this scenario 13% of the total calf production came from 2-year-old females. However, data from the Delta, Denali, and Porcupine (K. Whitten, this workshop) Herds suggest that survival of calves produced by 2-year-old females is lower than for calves produced by older cows. For example, Davis and Valkenburg (1981) determined that at least 2 of 6 calves born to 2-year-old cows in the Delta Herd survived to October in 1980, i.e., 233% survival compared with 58% for calves born to older females. In the Denali Herd in 1988 and 1989, 1 of 9 calves born to 2-year-old cows survived 15 days postpartum compared with 54% (37/68) of calves born to older females. K. Whitten (this workshop) reported that the 2 calves born to 2-year-old Porcupine Herd cows died within 24 hours of birth versus 71% survival until 1 July for calves born to older cows. L. Adams (unpubl. data) determined that, in 1988, birth weights were 25% lower for calves (n = 4) of 2-year-olds versus weights of calves born to >3-year-old cows, suggesting a possible explanation for the lower survival rate of the former calves. Hence an "adjustment" to the scenario assuming a survival rate of 0.5 for calves >3-year-olds and 0.25 to 0.13 for calves of 2-year-olds follows: (0.79) (0.9) (0.5) + (0.21) (0.5) (0.25) or (0.13) = 0.36 + 0.03 or 0.01. Therefore, 39 or 37 calves/100 cows would have survived, of which 8% or 3% were produced by 2-year-olds. In these scenarios, it is unlikely that early puberty would contribute more than 8% to the rate of herd growth (e.g., if r = 0.20 in an irrupting herd with high early puberty then r would = 0.18 without the contribution).

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