Alaska Department of Fish and Game
Division of Wildlife Conservation

Federal Aid in Wildlife Restoration
Research Progress Report

Distribution and Productivity of the Central Arctic Caribou Herd in Relation to Petroleum Development: Case History Studies with a Nutritional Perspective

by

Raymond D. Cameron

Project W-24-1
Study 3.35
December 1993

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PROGRESS REPORT (RESEARCH)

State: Alaska

Cooperators: U.S. Fish and Wildlife Service, University of Alaska-Fairbanks

Project No.: W-24-1 Project Title: Wildlife Research and Management

Study No.: 3.35 Study Title: Distribution and Productivity of the Central Arctic Caribou Herd in Relation to Petroleum Development: Case History Studies With a Nutritional Perspective

Period Covered: 1 July 1992-30 June 1993

SUMMARY

As of July 1992, the Central Arctic caribou (*Rangifer tarandus granti*) herd numbered approximately 23,400 head, confirming a decline in growth rate since the late 1970s and early 1980s. Aerial survey data obtained during the calving period from 1978 through 1987 demonstrate that maternal females and their calves were displaced outward after construction of the Milne Point road system. Data on radio-collared female caribou indicate that the likelihood of producing a calf is directly related to female body weight during the previous autumn, whereas both the incidence of early calving and the probability of calf survival are correlated with postpartum weight. Lower weight gains during summer among lactating than among nonlactating females substantially decreases parturition rate.

Key Words: Alaska, body weight, calving, caribou, Central Arctic herd, disturbance, nutrition, oilfield, reproduction.

CONTENTS

BACKGROUND

Reduced local use of calving and summer ranges by Central Arctic herd (CAH) caribou (*Rangifer tarandus granti*) has occurred with progressive oil development on the Arctic Coastal Plain (Cameron et al. 1979; Cameron and Whitten 1980; Smith and Cameron 1983; Whitten and Cameron 1983*a*, 1985; Dau and Cameron 1986). Habitat loss is, in itself, an undesirable consequence of petroleum development, but there is an additional major concern that such proximate impacts, operating cumulatively, will eventually result in reduced size and/or productivity of the herd through one or more possible mechanisms (Cameron 1983). Unfortunately, such concerns, though justified from a theoretical point of view, gain little empirical support from the literature. As industrial development in the Arctic is virtually unprecedented, there is little basis for predicting the extent and duration of habitat loss, much less the secondary short- and long-term effects on the well-being of a particular caribou herd.

These uncertainties form the basis of the present two-component study: (1) assessments of CAH productivity and distribution in relation to oilfield development; and (2) an investigation of the influence of female body condition on reproductive performance. Herein, I summarize or reference selected data obtained since 1987.

During this reporting period, a paper previously submitted to Canadian Journal of Zoology was accepted in revised form (Appendix A), another was presented as a poster at the Fifth Australasian Wildlife Management Society Conference (Appendix B), and a third is now in press, Journal of Mammalogy (Appendix C). After numerous delays, 13 years' road survey data on caribou distribution in relation to oilfield development west of the Kuparuk River have been summarized and submitted for publication as Wildlife Technical Bulletin No. 12. Finally, a new paper on predicting reproductive success of caribou from autumn body weight is in preparation for Journal of Wildlife Management (draft abstract, Appendix D).

OBJECTIVES

To monitor the size, calf production, and recruitment of the CAH.

To describe changes in the distribution and movements of CAH caribou in relation to oilfield development on the Arctic Coastal Plain.

To determine the relationship between body condition and reproductive performance of female caribou of the CAH, including comparisons of:

- the body condition, reproductive success, and offspring survival of females under disturbance-free conditions (i.e., east of the Sagavanirktok River) with the status of those exposed to oil-related development (i.e., west of the Sagavanirktok River); and
- the rates of summer weight gain and subsequent reproductive performance of lactating vs. nonlactating female caribou

RESULTS AND DISCUSSION

Status of the Central Arctic Caribou Herd

A July 1992 photocensus of the CAH yielded a total count of 23,400 (K. Whitten, unpubl. data), in general agreement with a point estimate of 19,000 made by extrapolation in June 1991 (D. Reed, unpubl. data). Both estimates indicate that the growth rate of the herd has, in recent years, declined from that noted in the late 1970s and early 1980s. In fact, had the CAH continued to increase at that previous rate, it would have numbered about 48,000 by 1992, roughly twice the observed total (Fig. 1). A reduced rate of growth is consistent with the downward trend in calf production based both on transect surveys of the calving grounds (Fancy et al. 1992) and on the reproductive success of radio-collared females (Fig. 2). All indications are that the CAH has reached or exceeded carrying capacity.

Development-related Changes in Caribou Distribution

Changes in the distribution of calving caribou associated with oilfield development have been quantified using strip-transect surveys flown by helicopter. As a follow-up to an earlier paper by Dau and Cameron (1986), Cameron et al. (1992*a*) showed that, following construction of a road system near Milne Point, mean caribou abundance declined by more than two-thirds within 2 km and nearly tripled 4-6 km from the road. Such perturbed distribution reduces the capacity of an area to support females and their calves. Logically, close spacing of roads within an oilfield complex may depress area-wide calving activity. That outward displacement of calving caribou from the Milne Point road system has occurred is corroborated by the regional changes in caribou distribution accompanying construction. Prior to road placement, caribou were found in a single, more-or-less continuous concentration roughly centered on the Milne Point Road; whereas a bimodal distribution, with one concentration each to the east and west of the road, was clearly apparent after construction (Smith and Cameron 1992).

A companion investigation conducted within the oilfield complex west of the Kuparuk River has been completed. For more than a decade, systematic surveys were conducted annually from that road system to monitor the influence of oilfield development on caribou distribution, group size and composition, movements, and road/pipeline crossing success. An overview of those results is to be published as a separate technical report (Smith et al. 1994).

Female Caribou Body Condition vs. Reproductive Performance

Body weight of female caribou in autumn is closely related to subsequent calving success (Appendix A). Radio-collared females that produced a calf were significantly heavier than those that did not; and the logistic regression relating parturition rate and autumn body weight was significant as well. In contrast, calving date and early calf survival are more closely correlated with maternal weight shortly after parturition. Females that calved on or before 7 June and/or whose calves survived at least 48 hours postpartum were significantly heavier in early July than those calving after 7 June and/or whose calves died within 48 hours; the corresponding logistic models also were significant. Hence, the likelihood of conceiving is, for the most part, a reflection of body condition at breeding, while parturition date and calf survival may be related to maternal condition during late gestation.

Comparative data on condition and reproductive success of females exposed to oil development west of the Sagavanirktok River vs. those under disturbance-free conditions to the east are, thus far, inconclusive. However, even though differences were not significant, some interesting consistencies emerged from the various analyses; July and October body weights, oversummer weight gain, the incidence of successive 2-year pregnancies, and perinatal calf survival were all lower for western than for eastern females (Cameron et al. 1992*b*). Additional analyses of the entire 1987-92 data set will be undertaken for the Final Report.

Mid- and late lactation exacts a substantial cost on summer weight gain which, in turn, influences the probability of conceiving that autumn. The lactating females comprising our sample averaged 9 kg less than nonlactating females, resulting in a projected 28% reduction in parturition rate (Appendix B). Thus, declining calf production of the CAH (Fig. 2) may be primarily a consequence of repeated failure to compensate for the metabolic burden of milk production (i.e., through increased forage intake or lower energy expenditure), thereby depressing body weights of females and evoking more frequent reproductive pauses (Appendix C).

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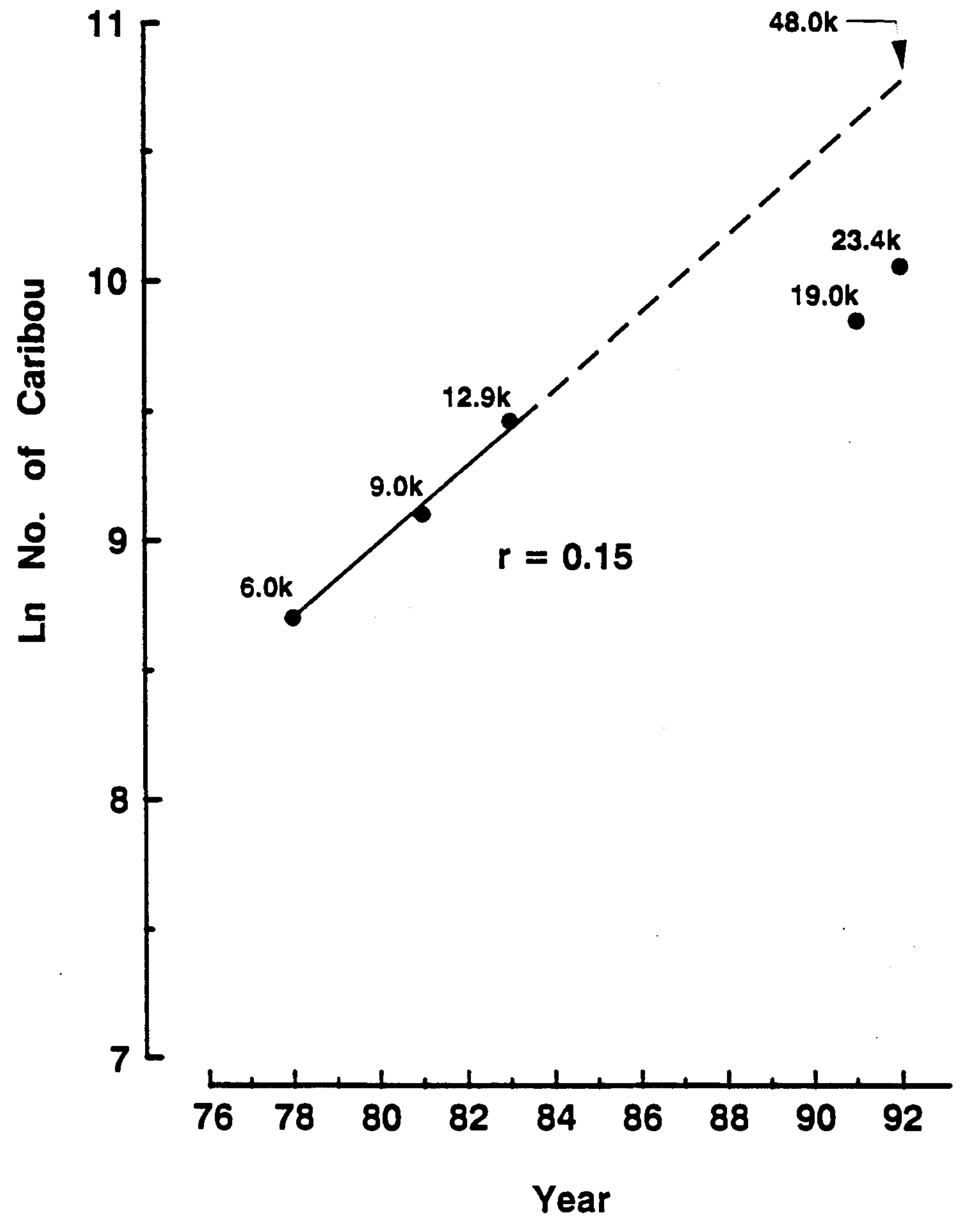

Fig. 1. Growth of the Central Arctic Caribou Herd, 1978-92. Census estimates by Whitten and Cameron (1983*b*), D. Reed (unpubl. data), and K. Whitten (unpubl. data).

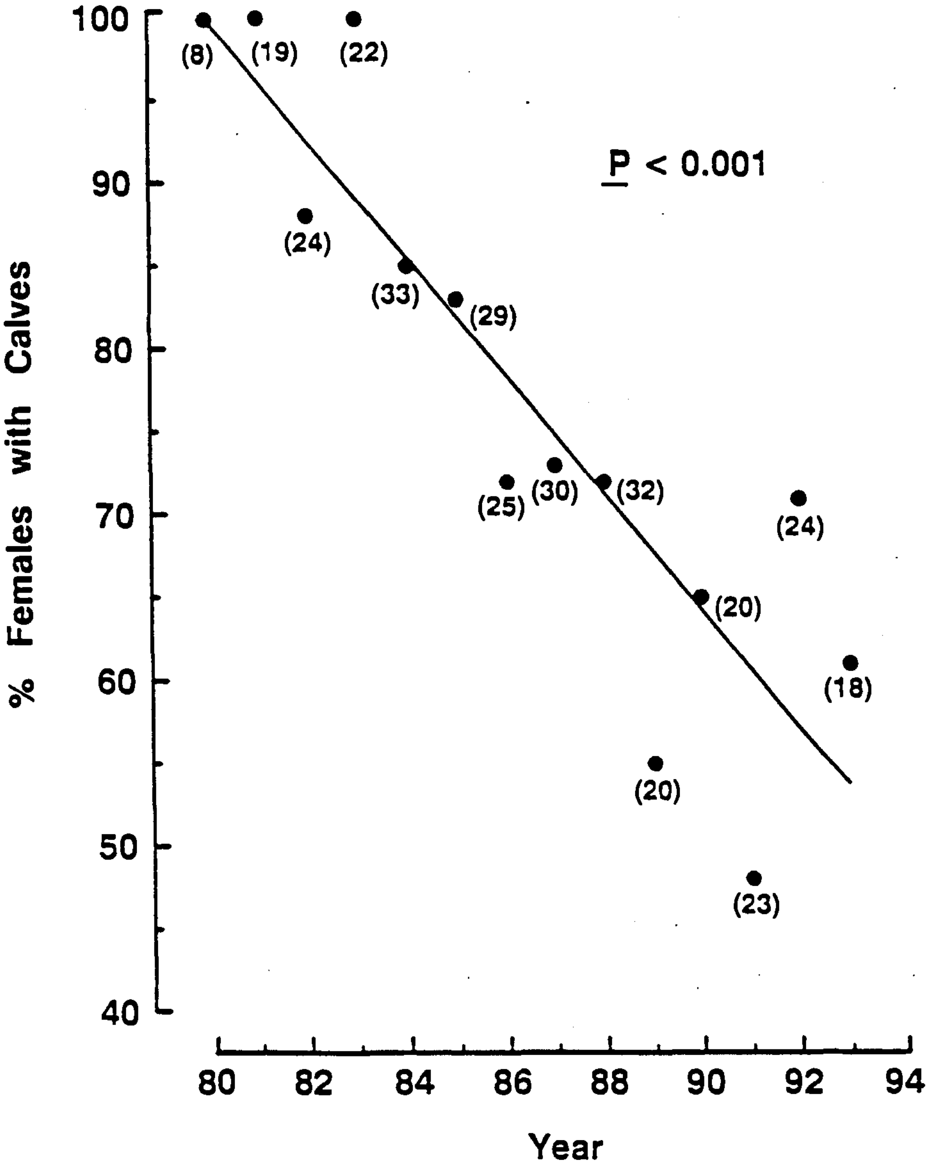

Fig. 2. Decline in calf production of the Central Arctic Caribou Herd, 1980-93. Estimates based on observations of radio-collared adult (i.e., sexually mature) females (*n*) from 10 June through 15 August. Note: Data not adjusted for east-west differences in herd productivity.

Appendix A. Manuscript published in Canadian Journal of Zoology 71:480-486 (1993)
(Minor reformatting for this progress report)

Calving success of female caribou in relation to body weight

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In late September and October 1987-90 and early July 1988-91, 66 radio-collared female caribou (*Rangifer tarandus granti*) of the Central Arctic Herd were captured and weighed 117 times. Caribou were relocated repeatedly during early June 1988-91; parturition status, calving date, and perinatal calf survival were determined. Mean autumn body weights of subsequently parturient (90.0 kg) and nonparturient (82.5 kg) females differed significantly ($P < 0.01$). Mean summer weights 4-5 weeks after parturition were significantly higher for females that had calved on or before 7 June (82.2 kg), rather than after 7 June (72.1 kg, $P < 0.01$); and for females whose calves survived at least 2 days postpartum (80.2 kg) vs. those whose calves died within 2 days (70.3 kg, $P < 0.01$). Significant logistic models were generated for relationships between parturition rate and autumn weight ($P < 0.01$), between the occurrence of early calving and summer weight ($P < 0.05$), and between calf survival rate and summer weight ($P < 0.02$). Body weight appears to be a reasonable index of body condition which, in turn, is related to reproductive performance. The probability of a successful pregnancy is largely predetermined at breeding based on autumn condition, whereas calving date and early calf survival appear to be influenced primarily by maternal condition during late pregnancy.

Introduction

The body condition of female reindeer and caribou (*Rangifer tarandus* spp.) at breeding appears to have a strong influence on subsequent reproductive success. Dauphine (1976) determined that body weight and fat content in autumn were higher among pregnant than among nonpregnant Canadian barren-ground caribou (*R. t. groenlandicus*), and Reimers (1983*a*) reported a positive relationship between pregnancy rate of wild reindeer (*R. t. tarandus*) and autumn dressed weight. Thus, females in good condition are more likely to ovulate and conceive than those in poor condition.

The timing of parturition may be a function of either autumn or overwinter condition. Reimers (1983*b*) reported that calving date of wild reindeer populations varied inversely with autumn dressed weight of adult females, suggesting that breeding may be initiated earlier if body reserves are sufficient for fetal development. Skogland (1983, 1984), however, related late calving to low food availability in winter. Calving date is influenced by nutrition (Bergerud 1975), but it is unclear if these differences are attributable to an effect on breeding date, gestation length, or both.

Perinatal calf survival has been linked to maternal condition during the previous winter. Skogland (1984) observed depressed fetal growth, low birth weights, and high rates of early calf mortality among wild reindeer following winter undernutrition. Offspring losses at or near parturition may occur either directly, through reduced viability of near-term fetuses or neonates (Skogland 1984), or indirectly through increased vulnerability to other forms of mortality (Dauphine 1976).

Thus far, investigations of the role of condition in the reproductive performance of free-ranging *Rangifer* have been based on carcass analysis, uterine/ovarian examination, or population-level estimates of calf production. Such methods preclude determination of the calving success of individual females after assessment of body condition. We report here on the reproductive performance of radio-collared Alaskan barren-ground caribou (*R. t. granti*) observed in June relative to their live weights during the previous September or October, and also during the following July. We show that parturition rate is closely related to autumn body weight (i.e., pre-rut condition), whereas both calving date and perinatal calf survival are better explained by summer weight (i.e., an index of condition during late gestation).

Methods

In late September and October 1987-90, 25 female caribou from the Central Arctic Herd (Cameron and Whitten 1979) were darted (3-4 mg Carfentanil citrate/100 kg, or 1-2 mg Carfentanil citrate with 19-42 mg Xylazine hydrochloride/100 kg) from a helicopter (Hughes 500D or Bell 206B), equipped with VHF transmitter collars (where appropriate), and weighed (Table 1) to the nearest kg using a net and tripod-mounted spring scale. Drug antagonists were then administered (150 mg Naloxone/mg Carfentanil citrate, intramuscular; 20 mg yohimbine, intravenous, as necessary, to enhance recovery from Xylazine hydrochloride), and the animal was released.

During late May and June 1988-91, each radio-collared female was relocated every 1-3 days by PA-18 Super Cub using standard telemetry techniques. Parturition status was ascertained by calf presence, or inferred from the timing of antler shedding and/or udder distension (Whitten 1991; Whitten *et al.* 1992). The calving date for each pregnant female was estimated from successive observations. Most maternal females were also relocated 1-3 times within 3-4 days after calving to identify any perinatal calf mortality, which was judged to have occurred if a calf was either observed dead or not seen with its dam during the 2-day period postpartum (Whitten *et al.* 1992).

Following calving in early July 1988-91, 62 females of known parturition status (i.e., collared females observed in June, or uncollared females with calves) were darted (2-5 mg Carfentanil citrate/100 kg, or 2-3 mg Carfentanil citrate with 21-53 Xylazine hydrochloride/100 kg), radio-collared (if appropriate), and weighed (Table 1), as described above.

Body weights in late September or October served as estimators of condition at breeding. Weights in early July were used as indices of condition during the calving season; in so doing, we assumed that weight changes during the 4-5 weeks after calving were similar for all females and reasonably constant across years.

Analyses were restricted to females observed with a calf at heel when collared or, in instances of recapture, those known to have calved previously. Mean body weights for the categories of parturition status, calving date (arbitrarily classified as occurring during or after the first week of June), and perinatal calf survival were compared using modified *t*-tests. Not all observations were independent, as some females were weighed more than once (Table 1). Therefore, the mean for each individual was computed as a ratio of the sum of the weights to the number of observations in a category, and a two-sample comparison was made (Cochran 1977:181). Relationships between reproductive variables and body weight were described by univariate logistic regression (SAS) based on the raw binary data:

$$\pi(x) = \frac{e^{b_0 + b_1 x}}{1 + e^{b_0 + b_1 x}} \times 100, \qquad (1)$$

where π is the percent probability of each response variable occurring at body weight x; logistic models were checked for goodness-of-fit (Lemeshow and Hosmer 1982). Collinearity between autumn and summer body weight was evaluated with Pearson's correlation coefficient. In all cases, *P*-values <0.05 were considered statistically significant.

Results

Autumn body weights of radio-collared caribou differed with respect to parturition status (Table 2). Females that subsequently produced calves were, on average, 7.5 kg heavier than those that did not. Weight differences in summer, however, were more closely associated with calving time and offspring viability. Mean weight of females that had calved during the first week of June was 10.1 kg higher than for those calving later in the month, and females with calves that had survived at least 48 hour postpartum averaged 9.9 kg heavier than those whose calves had died.

Mathematical models relating parturition rate, the incidence of early calving, and perinatal survival to body weight (Fig. 1, Table 3) were consistent with the above pattern of mean weights. A significant logistic regression for parturition rate was generated only when autumn body weight was used as the explanatory variable, despite collinearity between paired autumn and summer weights (n = 26, r = 0.68, P = <0.001). In contrast, significant models for both early calving and perinatal survival were based on summer body weight; paired weights were also collinear (n = 15 and 17, r = 0.72 and 0.71, P = <0.01 and <0.01, respectively).

Discussion

Parturition

Parturition rate may be closely tied to autumn body weight, in general agreement with previous reports of direct relationships between pregnancy or parturition rate and live or dressed weight of female barren-ground caribou (Dauphine 1976), wild reindeer (Reimers 1983*a*), and domestic reindeer (Eloranta and Nieminen 1986) in autumn. Similarly, pregnancy rate based on winter collections has been shown to vary directly with the intact or dressed weight of barren-ground caribou (Thomas and Kiliaan 1991), Peary caribou (*R. t. pearyi*) (Thomas 1982), and domestic reindeer (Lenvik *et al.* 1988). Body fat or protein content, rather than body weight itself, may influence breeding success (Thomas 1982; Adamczewski *et al.* 1987; Allaye-Chan 1991) through an effect on ovulation (Leader-Williams and Rosser 1983), although the metabolic mechanism is largely unknown (Ryg 1986); a possible nutritional signal or modulator to the endocrine system is an increased supply of branched-chain amino acids (Downing *et al.* 1990). Conception might also be implicated. Dauphine (1976) concluded that depressed ovulation occurred principally in young ($\leq$4-year-old) female caribou, whereas failure to conceive following ovulation or resorption of the fertilized ovum was the usual cause of infertility in older females.

The highly significant relationship between parturition rate and autumn body weight (Table 3) constitutes indirect evidence that rates of *in utero* mortality were low. As well, mean summer weight did not differ with parturition status (Table 2), nor did parturition rate vary over the observed range of summer body weights (Fig. 1), suggesting that fetal development proceeded irrespective of female condition during late gestation. Both Dauphine (1976) and Reimers (1983*a*) reported negligible fetal losses, and D. E. Russell (Canadian Wildlife Service, pers. comm.) noted that all 16 radio-collared females of the Porcupine Herd, determined to be pregnant in November 1990, calved in June 1991. In contrast, Skogland (1984) suspected higher *in utero* mortality among wild reindeer in a high-density population, and Gates *et al.* (1986) reported probable abortions among some barren-ground caribou on Coats Island following winter starvation. Hence, prenatal mortality may occur under severe circumstances, but it appears that conception and parturition rates are effectively equivalent. While the possibility of abortion or premature births resulting from chronic undernutrition cannot be ruled out, such mortality is ostensibly uncommon, at least for mainland *Rangifer* populations under conditions similar to those in our study.

Although autumn body weight, as an index of condition at breeding, is an important determinant of the likelihood of conceiving and carrying a fetus to term, age-dependent effects are also possible. By restricting our analysis to fecund females (see Methods), we eliminated any condition-unrelated complications associated with the age of first reproduction. However, this did not entirely preclude the possibility of an age effect, as young females may be less productive, regardless of body weight. Reimers (1983*a*) suspected that the pregnancy rate of yearling reindeer was lower than expected on the basis of autumn dressed weight, but reported that all females $\geq$3 years of age at breeding conformed with mathematical predictions of pregnancy rate based on weight alone. No yearlings (identified by immature facial structure and lanky conformation) were included in our sample of females, but it is conceivable that 2-year-olds (i.e., 28 and 37 months old in October and July, respectively) were overrepresented in the nonparturient category. If so, the logistic regression would have shifted to the right (Fig. 1), resulting in consistent underestimates of π (Equation 1).

In reality, though, serious errors of this nature are unlikely because fecundity is principally age-independent. Thomas and Kiliaan (1991) reported that, over an 8-year period, ranges in the pregnancy rate of Beverly Herd caribou were 0-33%, 47-100%, and 75-100% for females 1, 2, and $\geq$3 years of age, respectively. Such high variability renders age unreliable as a covariate for predictive purposes. Body weight or condition does not necessarily track age but varies in response to environmental factors that affect nutrition. In fact, it seems likely that short-term differences in the birth rate of a herd are more a consequence of condition-induced variations in fecundity within an age class than changes in the overall age distribution of females.

Calving date

A direct relationship between the incidence of early calving and female body condition during the following July (Fig. 1) indicates that maternal undernutrition late in gestation might delay parturition, a view supported by other work. In experiments on penned reindeer, Espmark (1980) noted that underfed females calved several days later than well-nourished controls. Similarly, Skogland (1983) reported later calving by wild reindeer following winters of deep, persistent snow when females were in poor condition, and suggested that parturition is postponed until the fetus attains a certain critical size. Bergerud (1975) concluded that breeding dates of caribou vary little between years and that variable calving dates may result from nutritionally related differences in gestation length. In the Central Arctic Herd, median calving date for all radio-collared females was 12 June in 1989, following a winter of deep snow, compared with 3-5 June in 1988, 1990, and 1991 when snowfall was considerably lower (R. Cameron, unpubl. data). These observations imply that winter--rather than summer--nutrition exerts the primary influence on the timing of parturition, a mechanism consistent with findings for other cervids (Bowyer 1991).

Alternatively, body condition at or near breeding may alter calving date via an effect on conception time. Baskin (1970) noted that "poorly fattened" domestic reindeer ovulate later than those in the best condition, and Reimers (1983*b*) reported a significant inverse relationship between mean autumn dressed weight of females and median calving date in eight populations of wild reindeer. Based on data from reindeer slaughtered approximately 4 months post-rut, Lenvik (1988) obtained inverse correlations between conception date (estimated from fetal age, Roine *et al.* 1982) and female dressed weight. However, Dauphine and McClure (1974), employing a similar approach for barren-ground caribou, found no relationship between conception date and either body weight or fat content.

The mechanism by which the timing of parturition varies is therefore uncertain. Our data and the results of several other studies suggest that date of calving is a function of the nutritional status of the gravid female, but we cannot discount the possibility of condition-related differences in the onset of ovulation. Logically, female condition prior to rut or during late gestation could be implicated, depending upon the timing of food limitation (Skogland 1984). For example, a particularly severe insect season might depress weight gain by autumn and delay ovulation, whereas undernutrition following conception would likely prolong gestation. Later calving would be the end result either way.

The genetic makeup and movement characteristics of *Rangifer* populations may also influence the timing of parturition, independent of nutritional status. Norwegian wild reindeer originating from domestic stock generally calve earlier than their truly wild counterparts; and, within a genetic line, calving tends to be earlier for migratory than for resident reindeer (Skogland 1983).

The consequences of delayed parturition are potentially serious. Whitten *et al.* (1992) found that caribou calves born after the peak of calving experienced higher mortality than those born before or during peak calving. Furthermore, as high-quality summer forage is available for only a brief period (Klein 1970; White *et al.* 1975; White and Trudell 1980), the timing of birth may be crucial to the developing calf. Late-born calves have less opportunity for growth before the onset of winter (Baskin 1970; Bergerud 1975; Skogland 1983, 1985) and are therefore more likely to suffer mortality due to predation and undernutrition (Dauphine and McClure 1974; Bergerud 1975; Couturier *et al.* 1990). Finally, females calving late might be unable to complete lactation in time to replenish body reserves by autumn, thereby reducing the chances of conceiving that year (Skogland 1985).

Calf survival

Among the caribou sampled, perinatal calf survival varied directly with the weight of females after calving. This relationship is consistent with other reports that maternal weight or food intake of *Rangifer* during late pregnancy is positively correlated with calf birth weight (Varo and Varo 1971; Bergerud 1975; Espmark 1980; Rognmo *et al.* 1983; Skogland 1984; Eloranta and Nieminen 1986; Adamczewski *et al.* 1987) and early survival (Rognmo *et al.* 1983; Skogland 1984; Eloranta and Nieminen 1986; Adamczewski *et al.* 1987). Evidently, if maternal reserves and food intake are insufficient to accommodate the increasing requirements of fetal growth (McEwan 1970; McEwan and Whitehead 1972; Robbins and Moen 1975; Oftedal 1985), a smaller, less viable neonate will be produced. Body protein content, in particular, appears to influence fetal and newborn weights of caribou (Allaye-Chan 1991; Allaye-Chan and White 1991).

The effect of calf birth weight on survival apparently extends beyond the perinatal stage. Domestic reindeer calves that survive the entire calving period (2-3 weeks) are heavier at birth than those that die (Eloranta and Nieminen 1986). Low weight at birth, and an associated low survival rate, may (Espmark 1980) or may not (Rognmo *et al.* 1983) be sustained through summer--depending upon both milk production, as influenced by maternal nutrition (White and Luick 1984; White 1991), and the degree of compensatory feeding possible on a given summer range (Rognmo *et al.* 1983; White 1991). Even surviving calves that remain small up to 6 weeks postpartum may be subject to higher mortality through autumn (Haukioja and Salovaara 1978).

Body weight as a condition index

Though statistically meaningful as an explanatory variable for caribou reproductive success, unadjusted body weight is not necessarily an accurate representation of body condition. Protein and fat content may vary independent of live weight (Allaye-Chan 1991; Allaye-Chan and White 1991), as can the contribution of alimentary fill (Cameron *et al.* 1975; Staaland *et al.* 1979; Adamczewski *et al.* 1987; White *et al.* 1987; Huot 1989), obscuring the interpretation of weight changes or differences. Variations in skeletal size introduce additional errors when body weight is used as the sole estimator of condition. It may be appropriate, therefore, to incorporate numerical condition scores with body weight determinations (Gerhart *et al.* 1992) or to scale body weight according to one or more morphometric measurements (Huot 1988).

Inaccuracies notwithstanding, the highly significant relationship between parturition rate and autumn body weight, in particular, is potentially of practical value in management of arctic caribou. If it can be demonstrated that the logistic regression applies to all females, and if the autumn weight distribution of females in the herd can be determined, an overall parturition rate can be predicted with some confidence. It is unlikely, however, that an equation developed for one population would apply to all others, especially those with vastly different genetic backgrounds (e.g., barren-ground vs. woodland caribou) or nutritional regimes (e.g., arctic vs. interior). Again, adjusting body weight for skeletal size should improve predictive power and broaden the application of these models. Such studies are in progress.

Acknowledgements

Financial support for this study was provided by Federal Aid in Wildlife Restoration, by the Alaska Department of Fish and Game, Division of Wildlife Conservation, and by the U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center. We thank R. A. DeLong, C. S. Gewin, H. N. Golden, E. A. Lenart, T. R. McCabe, L. M. McManus, D. C. Miller, D. J. Reed, R. T. Shideler, J. M. Suttie, J. M. Ver Hoef, and K. R. Whitten for technical assistance. R. K. "Fearless Fred" Friedrich, K. Jouppi, D. C. Miller, R. M. Warbelow, and R.D.C. served as pilots during one or more phases of this research. A. T. Bergerud, R. T. Bowyer, J. Huot, D. J. Reed, E. Reimers, and J. M. Ver Hoef critically reviewed the manuscript and offered helpful suggestions.

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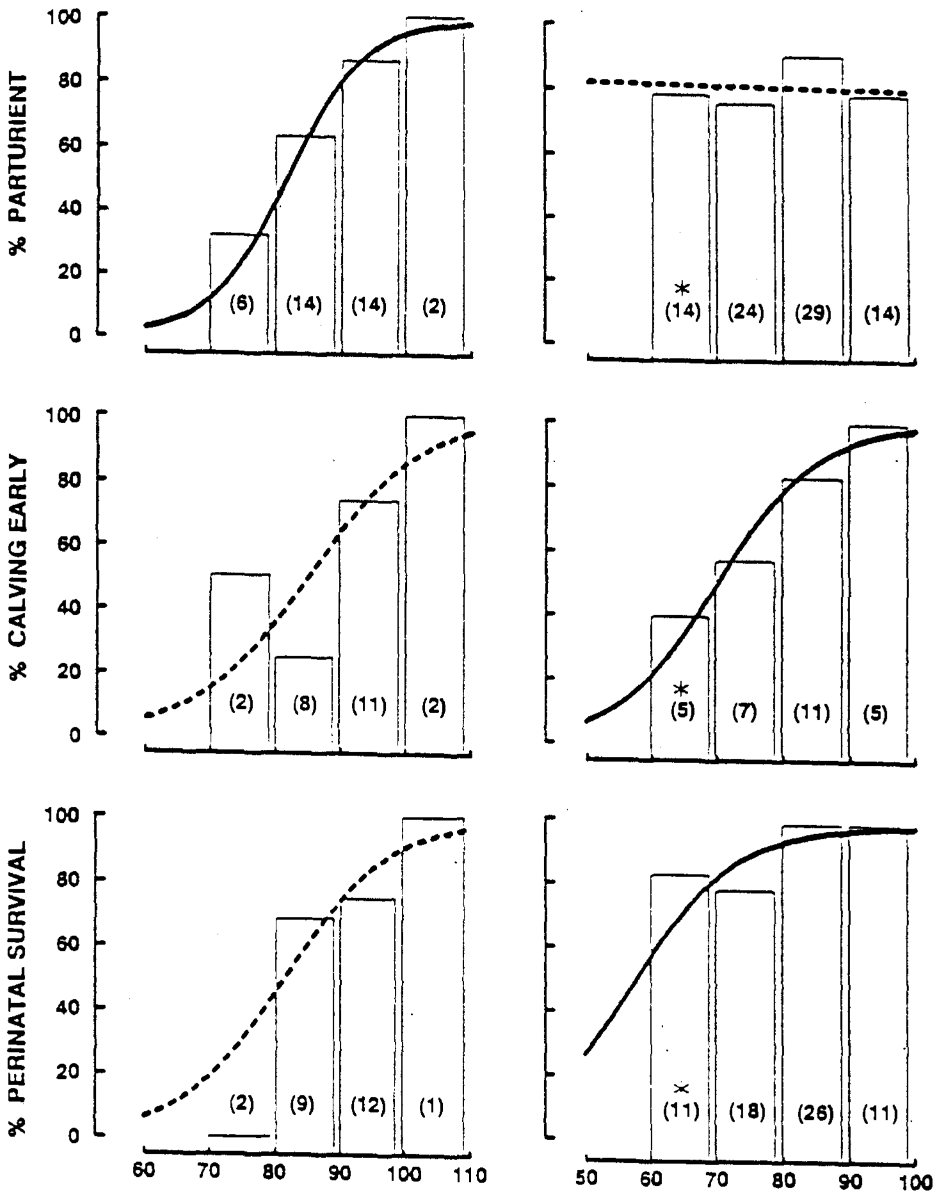

Fig. 1. Logistic regressions (solid lines are significant at $P < 0.05$; Table 3) of parturition rate, incidence of early calving (i.e., on or before 7 June), and perinatal (>2 days post partum) calf survival on autumn and summer body weights of female caribou, Central Arctic Herd, 1987-1991. The empirical percentages are shown at arbitrary 10-kg intervals of body weight; numbers in parentheses are sample sizes; the asterisk indicates inclusion of one female weighing 57 kg (Table 2).

TABLE 1. Numbers of adult female caribou from the Central Arctic Herd captured and weighed, 1987-1991

	Autumn		Summer	
Year	Inclusive dates	No. captured	Inclusive dates	No. captured
1987-1988	8-28 Oct.	13	2-4 July	20
1988-1989	23 Sept.-3 Oct.	9(5)	1-6 July	22(7)
1989-1990	26 Sept.-6 Oct.	10(4)	2-15 July	15(6)
1990-1991	4-7 Oct.	4(2)	9-13 July	24(6)
Total		36(11)		81(19)

Note: Parentheses enclose numbers of caribou previously captured one or more times within a season.

TABLE 2. Body weights of radio-collared female caribou from the Central Arctic Herd in autumn and summer relative to parturition status, calving time, and perinatal calf survival, 1987-1991

	Body weight, kg							
	Autumn				Summer			
	Mean ± SE	Range	*n*	*t*-test	Mean ± SE	Range	*n*	*t*-test
Parturient[a]	90.0 ± 1.2	78-106	25 (19)		79.3 ± 1.1	57-95	66 (57)	
Nonparturient[b]	82.5 ± 2.2	72-93	11 (10)	$P < 0.01$	79.5 ± 2.7	63-96	15 (14)	$P > 0.9$
Early calving[c]	92.4 ± 1.9	78-106	13 (12)		82.2 ± 2.0	63-95	20 (19)	
Late calving[d]	86.9 ± 1.4	78-93	10 (10)	$P < 0.05$	72.1 ± 3.0	57-84	8 (8)	$P < 0.01$
Perinatal survival[e]	90.8 ± 1.2	82-104	16 (13)		80.2 ± 1.1	62-95	60 (55)	
Perinatal mortality[f]	86.4 ± 1.9	78-91	8 (7)	$P < 0.1$	70.3 ± 3.8	57-79	6 (5)	$P < 0.01$

Note: Caribou were all fecund: calf at heel when collared, or known to have calved in a previous year. Parturition status was based on observations made during the June calving period, *n* is the number of weight observations (number of caribou).

[a] Calf at heel or distended udder observed.

[b] No calf at heel, no distended udder, and (or) antlers shed before 1 June.

[c] Calved on or before 7 June.

[d] Calved after 7 June.

[e] Calf alive ≥48 h post partum.

[f] Calf confirmed dead or not observed with its dam <48 h post partum.

TABLE 3. Parameter estimates of logistic models describing relationships between reproductive variables and body weight (see Fig. 1)

	Parameter estimate[b]							
	Autumn				Summer			
Response variable[a]	n	β_0	β_1	P	n	β_0	β_1	P
Parturient	36	-15.562	0.190	<0.01	81	1.686	-0.003	>0.9
Early calving	23	-17.893	0.203	<0.1	28	-9.115	0.130	<0.05
Perinatal survival	24	-17.874	0.210	<0.1	66	-7.282	0.127	<0.02

Note: P is the probability that $\beta_1 = 0$. There is no evidence for lack of fit.

[a] See Table 2.

[b] See eq. 1.

Appendix B. Poster presented at the Fifth Australasian Wildlife Management Society Conference, Brisbane, 2-4 December 1992.

(Reformatted for this progress report)

IMPORTANCE OF SUMMER WEIGHT GAIN TO THE REPRODUCTIVE SUCCESS OF CARIBOU IN ARCTIC ALASKA

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Abstract: In early July and again in early October 1988-91, 36 different adult female caribou (*Rangifer tarandus granti*) of the Central Arctic Herd were captured and weighed 92 times (i.e., 46 pairs of weights). For nonlactating females, July-October weight gain (y_i, kg) varied inversely with July body weight (x_i, kg): $y_i = --0.51\ x_i + 54.71$ ($r = 0.75$; $P < 0.001$); the hypothetical autumn "target" body weight (i.e., x-intercept) of 107 kg yields a 99% probability that a female will ovulate, conceive, and carry a fetus to term. For lactating females, however, that relationship was not significant ($P > 0.1$), and mean body weight by autumn was significantly lower than that of nonlactating females (85 vs. 94 kg, respectively; $P < 0.001$). The 9-kg difference in weight gain represents the net or "ecological" cost of mid- and late lactation, which would theoretically depress the parturition rate of the herd by 28%. Reduced fecundity probably results from repeated failure to compensate for the metabolic demands of lactation, thereby increasing the likelihood of breeding pauses.

Introduction

Annual patterns of weight gain and loss differ substantially between reproductively active and reproductively inactive female caribou (*Rangifer tarandus* spp.) (Fig. 1).

Oversummer (July-October) weight gain is particularly important, as the body weight attained at breeding in autumn (mid-October) bears directly on the probability of conceiving and carrying a fetus to term (Fig. 2).

We compare the autumn body weights of lactating and nonlactating female caribou relative to a theoretical "target" weight and discuss the implications to subsequent reproductive success.

Methods

In early July and again in early October 1988-91, 36 different adult female caribou of the Central Arctic Herd were darted from a helicopter, radio-collared (if uncollared), and weighed 92 times, yielding 46 pairs of weights.

Females with and without calves at heel in early July were classified as lactating and nonlactating, respectively. Each lactating female was relocated by fixed-wing aircraft at least once in late July or early August; those observed without calves were deleted from the sample.

Findings

For nonlactating females, summer weight gain varied inversely with summer body weight (Fig. 3). The hypothetical autumn "target" body weight was 107 kg. According to our logistic model (Fig. 2), females at 107 kg in autumn have a 99% probability of becoming pregnant and producing a calf.

For lactating females, the relationship was not significant (Fig. 3), and all points fell below the regression line for nonlactating females. However, a weak inverse correlation was apparent, suggesting a similar target mechanism.

Overall, few females achieved their hypothetical weight goals: no lactating females and only 5 (22%) nonlactating females exceeded 100 kg by autumn.

Autumn weights of lactating females were significantly lower than those of nonlactating females (Fig. 4). The mean 9-kg difference represents the net or ecological cost of mid- and late lactation, which translates into an estimated 28% reduction in parturition rate (i.e., from 0.86 to 0.62) (Fig. 5).

Conclusions

The disparity between the postcalving body weight of female caribou and a preferred target autumn weight appears to influence summer weight gain.

Few females of the Central Arctic Herd, be they lactating or nonlactating, attain autumn weights that virtually ensure subsequent parturition, suggesting that forage resources are limiting in most years or that other environmental factors (e.g., insects) preclude maximum intake and assimilation of nutrients.

Repeated failure to compensate for the metabolic costs of milk production may progressively reduce autumn body weights of individual females and, in so doing, evoke breeding pauses. And in fact, periodic cessation of reproductive activity is not uncommon in the Central Arctic Herd. Among 46 radio-collared females monitored for 2-4 years from 1989 through 1992, the mean parturition rate was 72% (R. Cameron, unpubl. data).

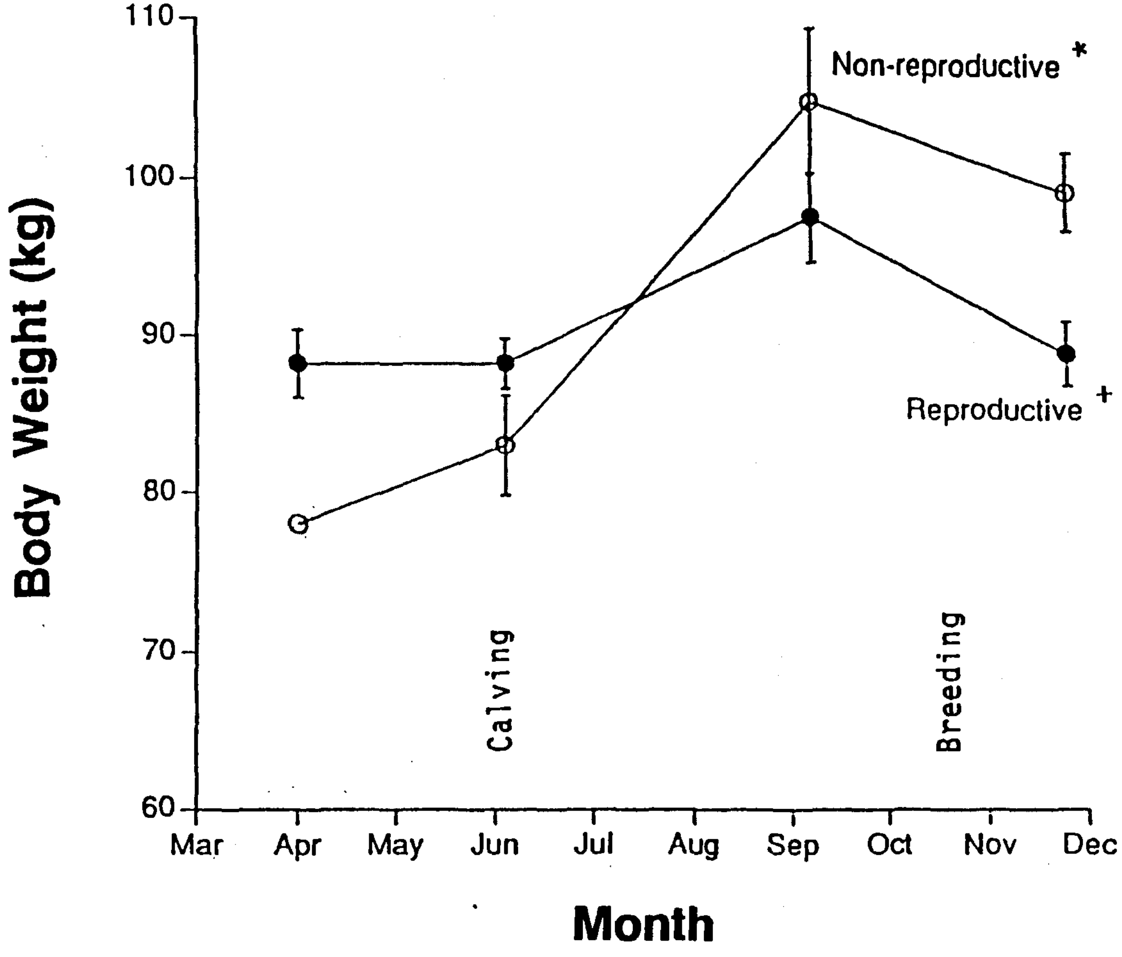

FIG. 1. Seasonal mean (±SE) body weights of reproductively active and reproductively inactive female caribou, Porcupine Herd.

* Pregnant in March/April, calving in June, lactating in September, and weaning in November.

\+ Failed to conceive or failed to lactate because of calf loss.

Adapted from Fig. 2, Allaye-Chan 1991 (Ph.D. Thesis, University of Alaska Fairbanks)

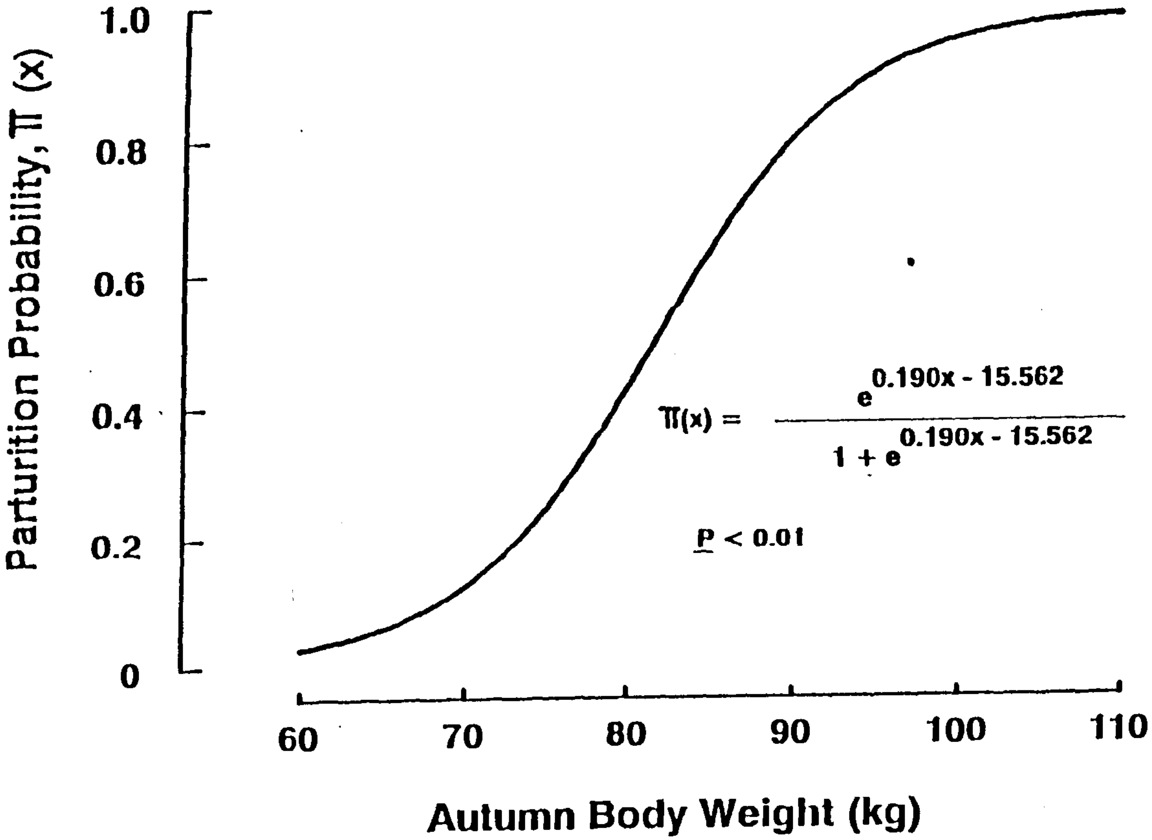

FIG. 2. Logistic regression describing the relationship between parturition probability and autumn body weight of female caribou. Adapted from Fig. 1, Cameron *et al.* 1993 (Can. J. Zool. 71:480-486).

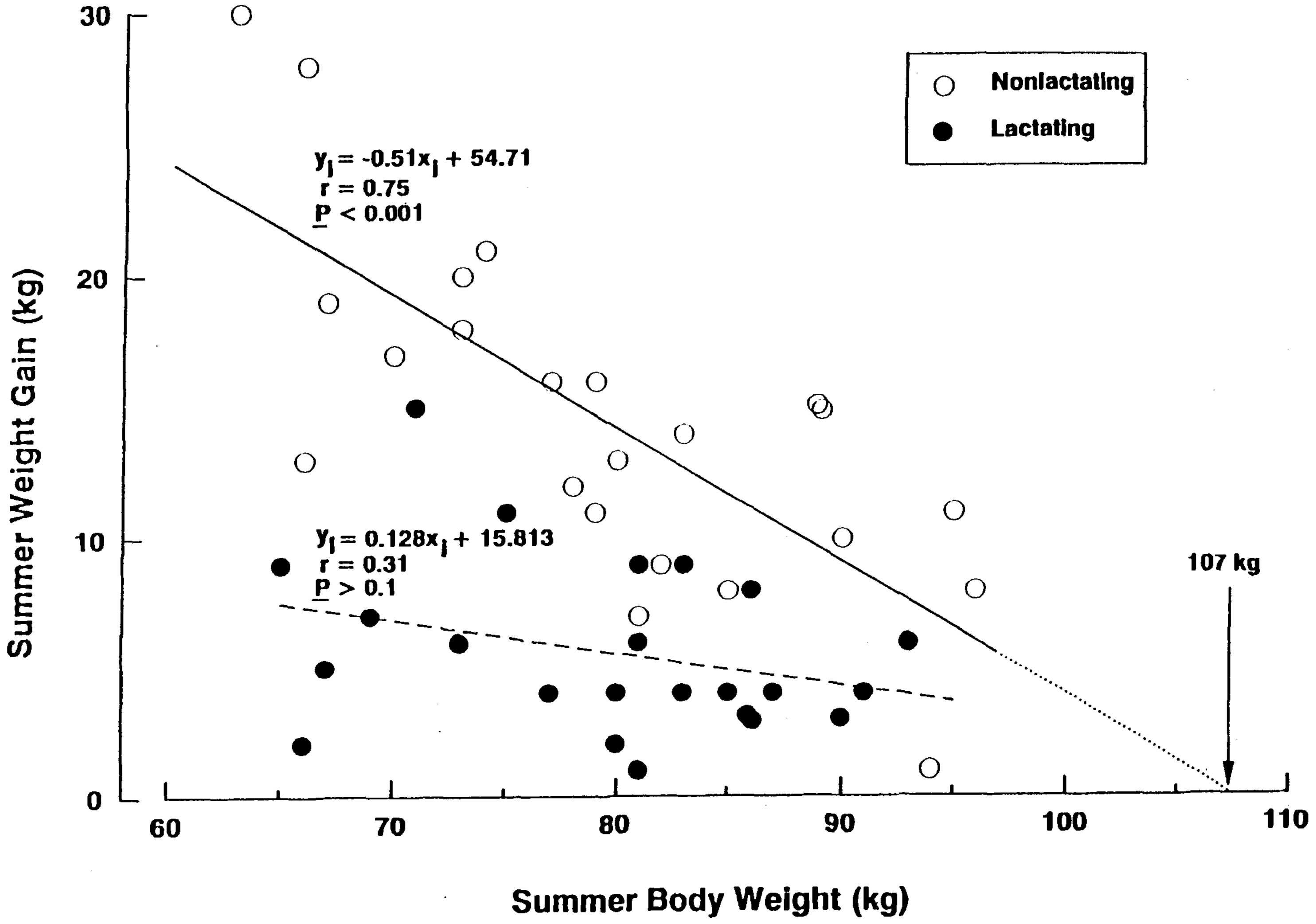

FIG. 3. Relationships between oversummer (July-October) weight gain and summer (July) body weight of lactating and nonlactating female caribou. The X-intercept of 107 kg is the theoretical autumn (October) "target" body weight (i.e., the summer weight at which subsequent gain is zero).

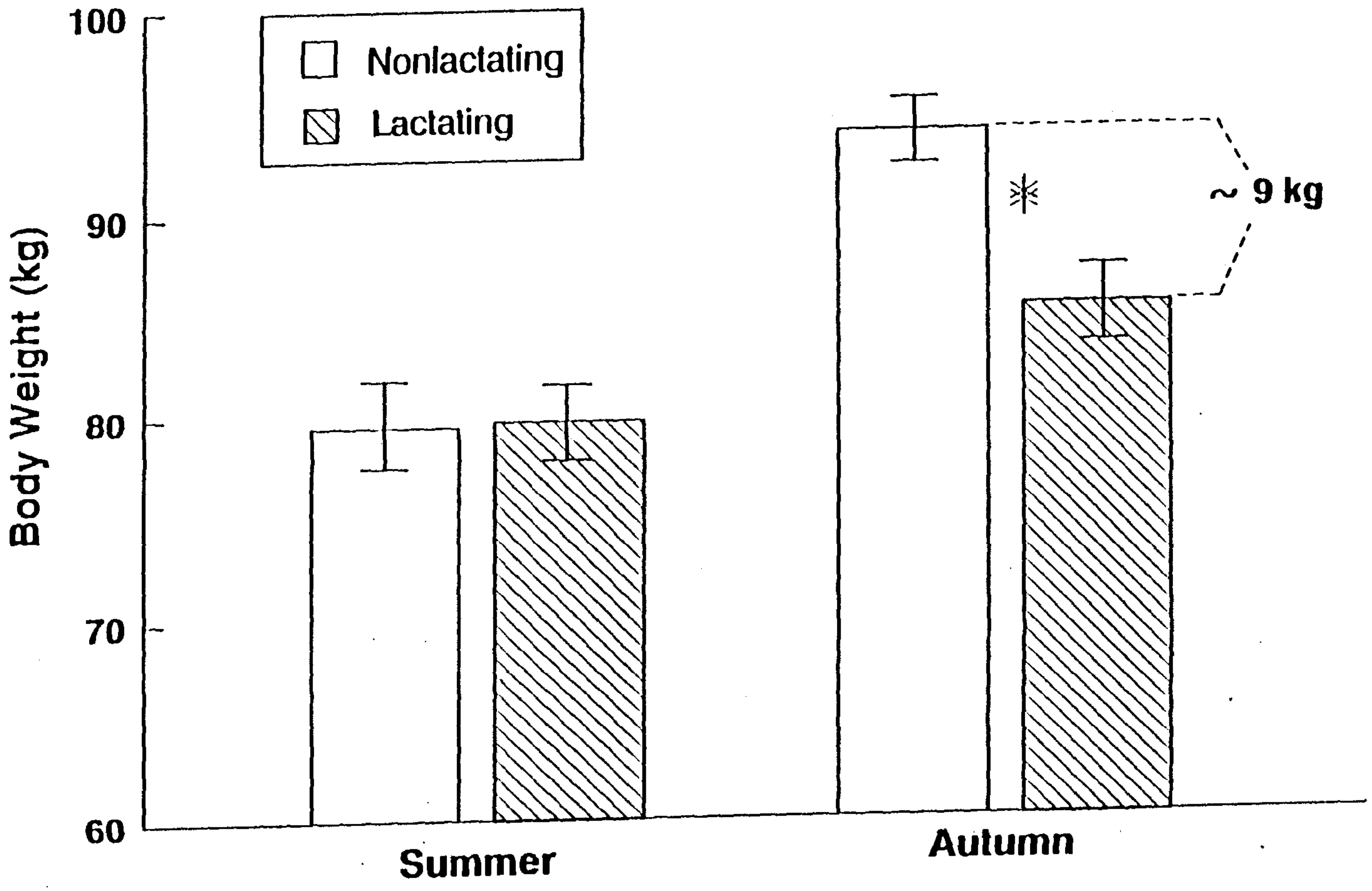

FIG. 4. Mean (±SE) body weights of lactating and nonlactating female caribou in summer (July) and autumn (October). * Significant at $P < 0.001$.

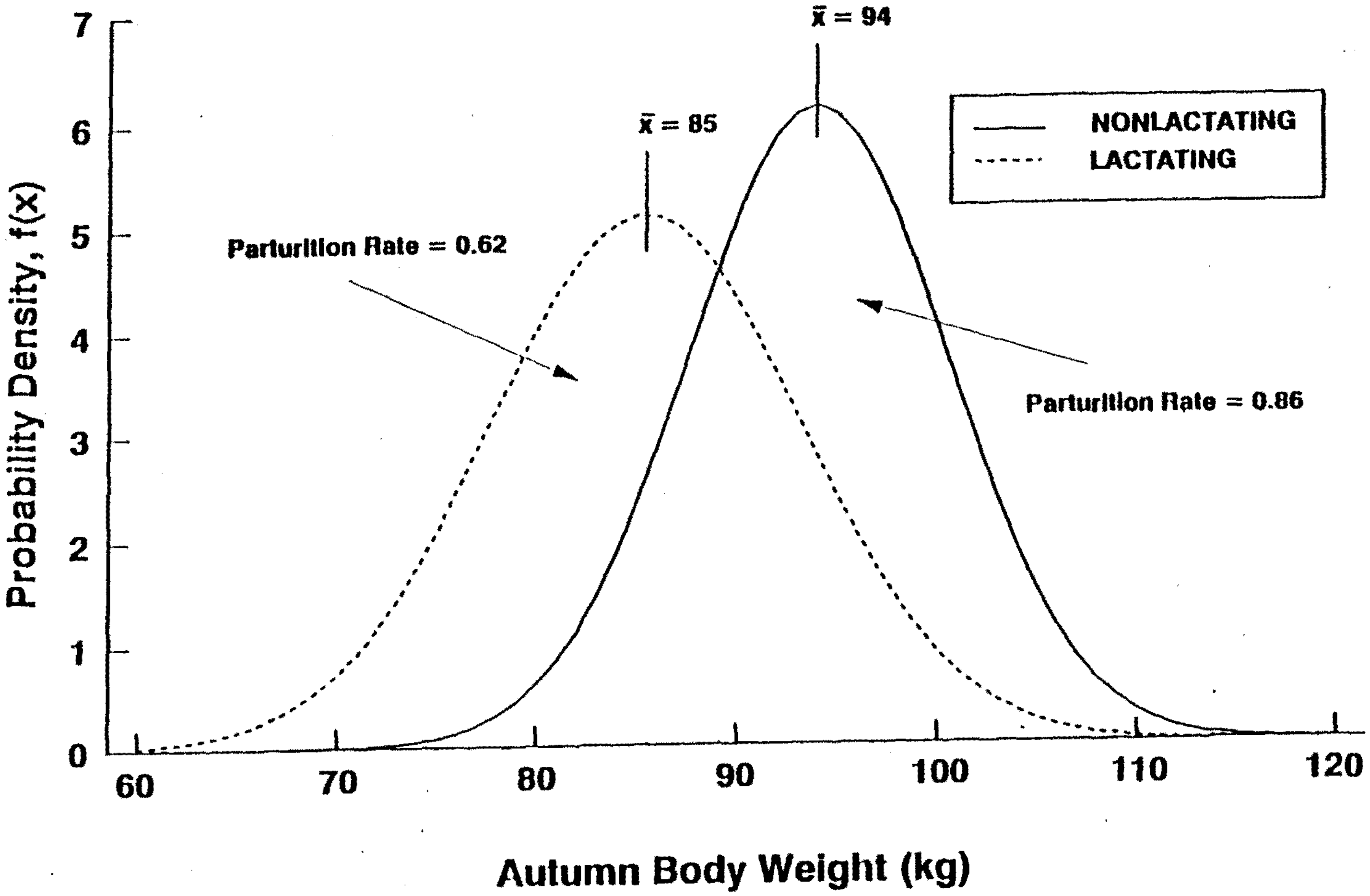

FIG. 5. Distributions of observed autumn (October) body weights for lactating and nonlactating female caribou. The associated parturition rates are integrated estimates derived from the logistic model (Fig. 2).

Appendix C. Manuscript to be published in Journal of Mammalogy (in press)
(Minor reformatting for this progress report)

REPRODUCTIVE PAUSES BY FEMALE CARIBOU

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Parturition status of 53 radio-collared female caribou (*Rangifer tarandus granti*) of the Central Arctic Herd was determined through repeated observations by fixed-wing aircraft during 2-5 calving periods. The overall frequency of reproductive pauses for females that were initially parturient, or previously confirmed to be parturient, was 24% (ca. once every 4 years). Most pauses preceded (78%) and followed parturition events (87%). Periodic infertility, as a response to nutritional stress, may enhance long-term reproductive performance in caribou and other ungulates.

Key words: caribou, *Rangifer tarandus*, reproductive pause, Alaska

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The notion that some female reindeer and caribou (*Rangifer tarandus* sp.) periodically fail to reproduce enjoys both empirical and theoretical support. Owing to a direct relationship between autumn body condition and pregnancy rate (Allaye-Chan, 1991; Cameron et al., 1993; Dauphine, 1976; Eloranta and Nieminen, 1986; Reimers, 1983), inability to compensate for the metabolic costs of gestation and lactation will eventually evoke a reproductive pause. By regressing the number of ovarian scars from corpora lutea on age of Canadian barren-ground caribou (*R. t. groenlandicus*), Dauphine (1976) showed that a female, once pregnant for the first time, averaged one pause every 5 years. Reimers (1983) reported that pregnancy and lactation depressed autumn body mass of wild Norwegian reindeer (*R. t. tarandus*) by 10-13% (relative to nonparous females), and postulated that repeated reproduction would therefore result in a "pregnancy resting" year.

Published accounts of multi-year reproductive success of wild *Rangifer* are surprisingly few. To my knowledge, only Davis et al. (1991) have provided long-term data from which periodic infertility of Alaskan barren-ground female caribou (*R. t. granti*) can be demonstrated. Here, I provide additional evidence that reproductive pauses can and do occur in free-ranging caribou and discuss the implications for population productivity.

METHODS

In conjunction with studies of body condition of caribou in northern Alaska, the reproductive success of 53 radio-collared female caribou of the Central Arctic Herd (Cameron and Whitten, 1979) was determined for 2-5 years. Caribou were relocated every 1-3 days by fixed-wing aircraft during early June 1988-1992. Parturient females were identified based on presence of a calf or through observations of retained antlers and distended udders (Whitten, 1991; Whitten et al., 1992). Unless known to have calved before 1988, females were added to the sample beginning in the year they were confirmed to be fecund. Mean frequencies of reproductive pauses were calculated as cumulative ratios (Cochran, 1977). Ages refer to those at calving.

RESULTS AND DISCUSSION

Of 134 determinations of parturition status over the 5-year period, 32 were negative (Table 1), yielding a reproductive pause frequency of 24% (binomial 95% CI, 17-32%). If younger females with a lower incidence of successive 2-year pregnancies (Dauphine, 1976) were inadvertently included, there was no detectable influence on the outcome, because the frequencies of pauses for 53 females $\geq$3 years old, 21 females $\geq$4 years old, and 12 females $\geq$5 years old (based on time since initial collaring and assuming none were <3 years old in year 1) were 24, 28, and 33%, respectively. Disturbance during capture had no measurable effect; 30 females that had been captured and weighed during at least 1 autumn before a calving period had a pause frequency of 26%, compared with 20% for the other 23 females (χ^2, P > 0.5).

A 24% pause frequency for the Central Arctic Herd is not dissimilar to Dauphine's (1976) estimate of 20% (1 year in 5) for the Kaminuriak Herd of mainland Canada. In contrast, an analysis of data on known-age females of the Delta Herd of interior Alaska (Davis et al., 1991) indicates a 5-year average of 11%. That lower value may be a consequence of high rates of early calf mortality, which prematurely releases females from the metabolic burden of lactation, thereby promoting summer weight gain and increasing the likelihood of conception in autumn (Davis et al., 1991).

For most females of the Central Arctic Herd, reproductive pauses preceded (78% of 18) and followed parturition events (87% of 31). Likewise, Dauphine (1976) reported that $\geq$4-year-old females from the Kaminuriak Herd, if not pregnant during the previous year, conceived in the year they were collected; and that failure to breed almost always followed a pregnancy. Similarly, Davis et al. (1991) showed that reproduction among fecund females of the Delta Herd was interrupted by only single years of infertility. One year of recuperation apparently is sufficient to allow resumption of breeding.

There were two exceptions to this 1-year rule. In 5% of 81 total pairs of consecutive observations, an instance of reproductive inactivity was followed by another. One female, accompanied by a calf when collared in autumn 1988, failed to produce a calf for the next 2 years; she was found dead in spring 1991. A second female, with a calf when captured in late spring 1987, was nonparous for 4 consecutive years thereafter; she was pregnant again in 1992, but the calf died within 2 days of birth. These represent the only known multiple pauses for the Central Arctic Herd since tracking began in the late 1970s.

My data corroborate other reports of a low incidence of chronic infertility in caribou (Dauphine, 1976; Davis et al., 1991; Thomas and Barry, 1990). The logical inference is that observed reproductive inactivity among a portion of the adult females in a herd is primarily attributable to the occasional collective pauses--and not clinical barrenness--of individuals.

Factors controlling the birth rate of a caribou population are overwhelmingly of nutritional origin. The number of adult females that are parturient (i.e., those not undergoing reproductive pauses) is a function of their body condition during the previous autumn (Allaye-Chan, 1991; Cameron et al., 1993; Dauphine, 1976). Fecundity of 2-year-olds varies considerably (Dauphine, 1976; Davis et al., 1991; Thomas and Barry, 1990), presumably also in response to changes in foraging success. Thus, depending upon nutrient balance before breeding, reproductive pauses by adults may be either postponed or elicited, and the onset of puberty by juveniles may be either expedited or delayed. Unusually adverse conditions (e.g., a severe insect season) would depress overall reproductive success for that year through a tendency to synchronize adult pauses and reduce the number of pubescent juveniles.

Periodic infertility is ostensibly widespread among ungulates. Variable calf production in adult female elk and red deer (*Cervus elaphus*; Clutton-Brock et al., 1982; Taber et al., 1982), mule deer (*Odocoileus hemionus*; Bowyer, 1991), moose (*Alces alces*; Gasaway et al., 1992), and Dall's sheep (*Ovis dalli*; Heimer and Watson, 1986; Rachlow and Bowyer, 1991) implies that reproductive pauses occur in these species as well. Confirmation will require frequent monitoring of collared individuals during the birthing period and documenting instances of reproductive inactivity following one or more known pregnancies. Only then can a clear distinction be made between nonbreeding adults and prepubescent juveniles.

Reproductive pauses in response to dietary insufficiency may have considerable adaptive value. Failure to ovulate or conceive when maternal reserves are inadequate for fetal development minimizes wasted reproductive effort and virtually ensures timely birth of a viable neonate the following year. Indeed, foregoing an unsuccessful pregnancy might provide nutritional relief that is sufficient to defer a subsequent pause, resulting in the production of at least one additional offspring over the long term.

ACKNOWLEDGMENTS

This study was funded by Federal Aid in Wildlife Restoration, the Alaska Department of Fish and Game, and the U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center. I thank C. S. Gewin, K. Jouppi, L. M. McManus, W. T. Smith, and R. M. Warbelow for technical assistance. J. M. Ver Hoef assisted with statistical analyses. R. T. Bowyer, D. J. Reed, R. G. White, K. R. Whitten, and two anonymous referees provided helpful comments on earlier drafts of the manuscript.

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Submitted, 8 February 1993.

Table 1.--Frequency of reproductive pauses for 53 radio-collared female caribou[a] of the Central Arctic Herd, Alaska, 1988-1992.

Number of females	Consecutive years observed	Female-years observed	Female-years nonreproductive
33	2	66	12
14	3	42	13
4	4	16	1
2	5	10	6
53		134	32

[a] All fecund: confirmed parturient or known to have calved previously.

Appendix D. Abstract of manuscript in preparation for Journal of Wildlife Management.

PREDICTING REPRODUCTIVE SUCCESS OF CARIBOU FROM AUTUMN BODY WEIGHT

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JAY M. VER HOEF, Alaska Department of Fish and Game, 1300 College Road, Fairbanks, AK 99701

Abstract: We evaluated relationships between observed calving success of female barren-ground caribou (*Rangifer tarandus granti*) and their body weight during the previous autumn. Attempts to validate a published logistic regression for parturition rate (Cameron et al. 1993) and one for net calf production (i.e., parturition rate less perinatal mortality), using an independent 1991-92 sample of females, were unsuccessful; goodness-of-fit tests showed significant lack-of-fit ($\underline{P} = 0.0025$ and 0.0002, respectively). Adding metatarsal length (an index of skeletal size) as a covariate in multiple logistic regressions did not improve fit (both $\underline{P} = <0.0001$). However, logistic regression models for parturition rate and net calf production vs. body weight that included the 1991-92 samples were significant ($\underline{P} = 0.0251$ and 0.0111, respectively), with no evidence for lack-of-fit ($\underline{P} = 0.0534$ and 0.1157, respectively). Again, incorporating metatarsal length as an explanatory variable resulted in no improvement; likelihood ratio tests indicated that models based only on autumn weight were sufficient ($\underline{P} = 0.1196$ and 0.7757, respectively). These models may be useful as predictive tools for the Central Arctic Herd and for adjacent herds with similar nutritional regimes.

Errata: Please place as page 34 in Study 3.35 (Cameron, 1993).

Appendix D. Abstract of manuscript submitted to Journal of Wildlife Management.
(Minor reformatting for this progress report)

PREDICTING PARTURITION RATE OF CARIBOU FROM AUTUMN BODY WEIGHT

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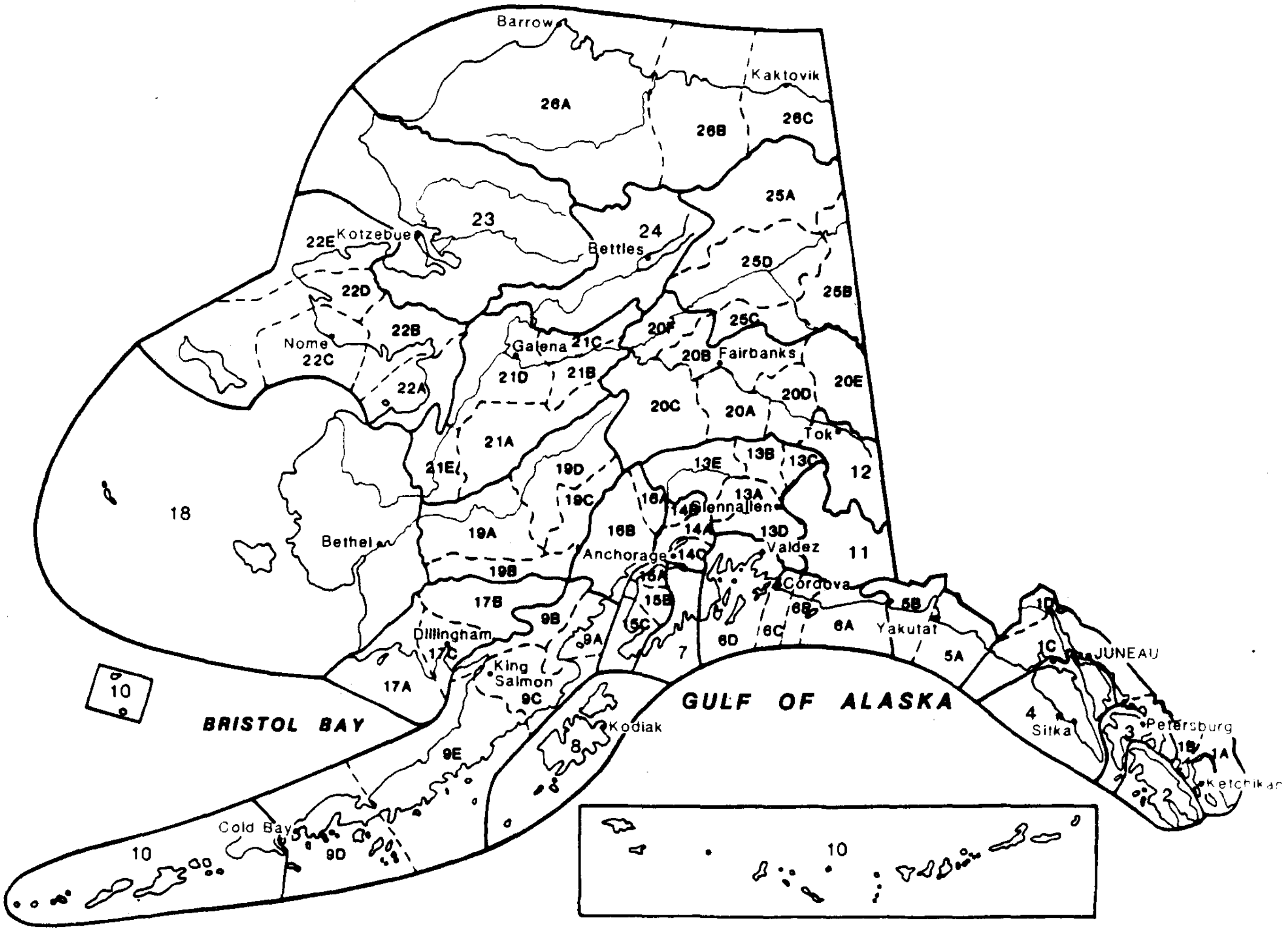
Abstract: We updated a logistic-regression model of the relationship between probability of parturition for adult caribou (*Rangifer tarandus granti*) and their body weight during the previous autumn using additional data obtained from 15 females. When all samples were combined, a significant year effect was not discernible ($P = 0.649$), so a new model was generated from the pooled data ($P = 0.025$). We also derived a model for parturition rate of the herd based on the logistic regression for individual females and the distribution of body weights. Small shifts in the weight distribution result in relatively large changes in parturition rate, emphasizing the importance of minor changes in forage quality and availability, and indicating a need for highly representative weight samples when attempting to predict parturition rate. Because of the difficulties in obtaining unbiased samples and the serious errors inherent in not doing so, we recommend estimating parturition rate directly by determining the reproductive status of a sample of radio-collared adult females, and through systematic antler and udder counts.

Alaska's Game Management Units



Federal Aid in Wildlife Restoration

The Federal Aid in Wildlife Restoration Program consists of funds from a 10% to 11% manufacturer's excise tax collected from the sales of handguns, sporting rifles, shotguns, ammunition, and archery equipment. The Federal Aid program then allots the funds back to states through a formula based on each state's geographic area and the number of paid hunting license holders in the state. Alaska receives 5% of the revenues collected each year, the maximum allowed. The Alaska Department of Fish and Game uses the funds to help restore, conserve, manage, and enhance wild birds and mammals for the public benefit. These funds are also used to educate hunters to develop the skills, knowledge, and attitudes necessary to be reponsible hunters. Seventy-five percent of the funds for this project are from Federal Aid.