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Federal Aid in Wildlife Restoration
Research Final Report
1 July 1987 - 31 August 1994

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

Grant W-23-1, W-23-2
W-23-3, W-23-4
W-23-5, W-24-1
W-24-2, W-24-3
Study 3.35
December 1994

Alaska Department of Fish and Game
Division of Wildlife Conservation
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FINAL REPORT (RESEARCH)

State: Alaska

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

Project No.: W-23-1, W-23-2, W-23-3, W-23-4, W-23-5, W-24-1, W-24-2, W-24-3 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 1987-31 August 1994

SUMMARY

As of July 1992, the Central Arctic caribou (*Rangifer tarandus granti*) herd numbered approximately 23,400 head, confirming a decline in growth rate; low calf production in recent years was a contributing factor. Aerial survey data obtained during the calving period demonstrate maternal females and their calves were displaced outward after construction of the Milne Point road system. Similar abnormalities in caribou distribution associated with oilfield development were observed in mid-summer. Data on radiocollared female caribou indicate 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. During summer lower weight gain among lactating than among nonlactating females substantially decreases parturition rate. The high frequency of reproductive pauses among females exposed to disturbance may be attributable to their relative inability to compensate for the metabolic costs of milk production.

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 oilfield 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 reduce productivity of the herd. Specifically, displacement of adult females from preferred areas could adversely affect foraging success and therefore growth and fattening (Cameron 1983; Elison *et al.* 1986; Clough *et al.* 1987), which in turn might depress calf production (Dauphinè 1976;

Thomas 1982; Reimers 1983; Eloranta and Nieminen 1986; Lenvik *et al.* 1988; Thomas and Kiliaan 1991) and survival (Haukioja and Salovaara 1978; Rognmo *et al.* 1983; Skogland 1984; Eloranta and Nieminen 1986; Adamczewski *et al.* 1987).

Such concerns, though justified from a theoretical point of view, lack empirical support. 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. Furthermore, despite a general acceptance that female body condition and fecundity are functionally related, it is unlikely that any single model would apply to all subspecies of *Rangifer*, and perhaps not even within a subspecies for different geographic areas. We therefore possess neither adequate foresight as to the probable behavioral responses of Arctic caribou to industrial development, nor an understanding of the mechanisms by which changes in habitat use might translate into measurable impacts on population dynamics.

These uncertainties form the basis of the present two-component study: (1) assessments of CAH productivity and distribution in relation to oilfield development; (2) an investigation of the influence of female body condition on reproductive performance. Here I summarize, extract, or update results from various reports and publications in addressing study objectives. Applicable methods, where not described, are detailed in the sources cited.

Under the auspices of this study and through a companion program at the University of Alaska Fairbanks, 8 manuscripts have been published, and 10 others are currently in preparation (Appendix A). During the past year, a paper on predicting parturition rate of caribou was accepted by the Journal of Wildlife Management (Appendix B), another on abundance of radiocollared caribou near Prudhoe Bay was submitted to *Rangifer* (abstract, Appendix C), and a note on measurements of weight vs. mass was accepted for publication in the fall 1994 issue of the Wildlife Society Bulletin (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 the growth rate of the herd has 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 low calf:cow ratios estimated from transect surveys of the calving grounds (range, 48-74 calves/100 cows: Fancy *et al.* 1992; Cameron, unpubl. data) and a downward trend in the reproductive success of radiocollared females (Fig. 2). Preliminary analyses of weather data indicate the inferred decline in female body condition (Cameron *et al.* 1993) cannot be attributed to increasing trends in either insect activity or snow depth. The CAH apparently has reached or exceeded carrying capacity (Cameron and Bowyer, in prep. [B.5., Appendix A]).

Development-related Changes in Caribou Distribution

Changes in the distribution of calving caribou associated with the Kuparuk Development Area (KDA), west of Prudhoe Bay (Fig. 3), have been quantified using strip-transect surveys flown by helicopter (Fig. 4). As a follow-up to an earlier paper by Dau and Cameron (1986), Cameron *et al.* (1992*a*) showed that, after 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 roads (Fig. 5). Such perturbed distribution reduces the capacity of an area to support females and their calves. Logically, roads comprising an oilfield complex that are, on average, <3 km apart may depress area-wide calving activity; and, in fact, percent occurrence of caribou in the heavily-developed western portion of the KDA declined significantly from 1979 through 1987, independent of total abundance (Fig. 6). The probable consequences of perturbed distribution is reduced access to preferred habitats (Cameron *et al.* in prep. [B.4. Appendix A]; Nellemann and Cameron, in prep. [B.6., Appendix A]).

That outward displacement of 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 east and west of the road, was clearly apparent after construction (Fig. 7; Smith and Cameron 1992).

A companion investigation conducted from the KDA road system has been completed (Smith *et al.* 1994). During spring and summer 1978-90, the Spine and Oliktok Roads (Fig. 3) were surveyed systematically by light truck to monitor the influence of oilfield development on caribou distribution and movements. Caribou increasingly avoided zones of intensive activity, especially during the calving period. In addition, crossings of the road transect by large, insect-harassed groups shifted away from the central portions of the complex to areas of lower disturbance near Oliktok Point and the Kuparuk floodplain. Clearly, patterns of caribou use have changed considerably in recent years.

Female Caribou Body Condition vs. Reproductive Performance

Body weights of CAH female caribou are closely related to their reproductive success (Cameron *et al.* 1993). For radiocollared females, the probability of producing a calf varied directly with body weight during the previous autumn, in contrast to calving date and perinatal survival, which were more closely related to maternal weight shortly after parturition (Fig. 8). Probably the likelihood of conceiving is determined by body condition at breeding, whereas parturition date and calf survival are linked to maternal condition during late gestation. Body fat content, specifically, is highly correlated with fecundity (Gerhart *et al.*, in prep. [B.8., Appendix A]).

Several data sets suggest reduced nutritional status and reproductive success of radiocollared females exposed to oil development west of the Sagavanirktok River. July and October body weights, oversummer weight gain, the incidence of successive 2-year pregnancies, and perinatal calf survival were all lower for females to the west than for those under disturbance-free conditions to the east, although differences were not significant at the 95% confidence level (Cameron *et al.* 1992*b*). A recent longitudinal analysis of fecundity, however, showed the frequency of reproductive pauses was significantly higher for western (36%) than for eastern (19%) (*t*-test, $P < 0.02$). This is the subject of a future paper (Cameron, in prep. [B.10., Appendix A]).

Mid and late lactation exacts a substantial cost on summer weight gain which, in turn, influences the probability of conceiving that autumn (Cameron and White 1992). Weights of lactating CAH females averaged 9 kg less than for nonlactating females (Fig. 9), resulting in a projected 28% reduction in parturition rate (Fig. 10). Thus, declining calf production of the herd in general (Fig. 2), and among females west of the Sagavanirktok River in particular, may be 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 condition and evoking more frequent reproductive pauses (Cameron and Ver Hoef 1994, Appendix B).

ACKNOWLEDGMENTS

I am particularly grateful to W. T. Smith for his advice and support in all phases of this study, and to C. S. Gewin for skilled technical assistance in both field and office. S. G. Fancy, K. L. Gerhart, and R. G. White collaborated on several aspects of the field research and on manuscripts that are now published or in preparation. For additional technical assistance, I thank S. C. Bishop, G. M. Carroll, B. Griffith, R. G. Hunter, T. R. McCabe, R. T. Shideler, M. D. Smith, N. E. Walsh, K. R. Whitten, and J. F. Winters. I also thank pilots D. C. Miller, R. K. Friedrich, and R. M. Warbelow for their skilled support. Special recognition goes to L. A. McCarthy and L. M. McManus for their invaluable assistance in preparing various reports and publications, and to R. A. DeLong, E. A. Lenart, D. J. Reed, and J. M. Ver Hoef for their efforts in data management, graphics, computer programming, and statistical analyses. Finally, thanks to T. R. McCabe, D. J. Reed, and W. L. Regelin for the dealing with the assorted administrative matters that I so deeply despise.

Financial support was provided by Federal Aid in Wildlife Restoration; by the Alaska Department of Fish and Game, Divisions of Wildlife Conservation and Habitat Restoration; and by the U.S. Fish and Wildlife Service, Alaska Fish and Wildlife Research Center. Numerous staff of the Alaska Department of Transportation and Public Facilities assisted frequently with field logistics.

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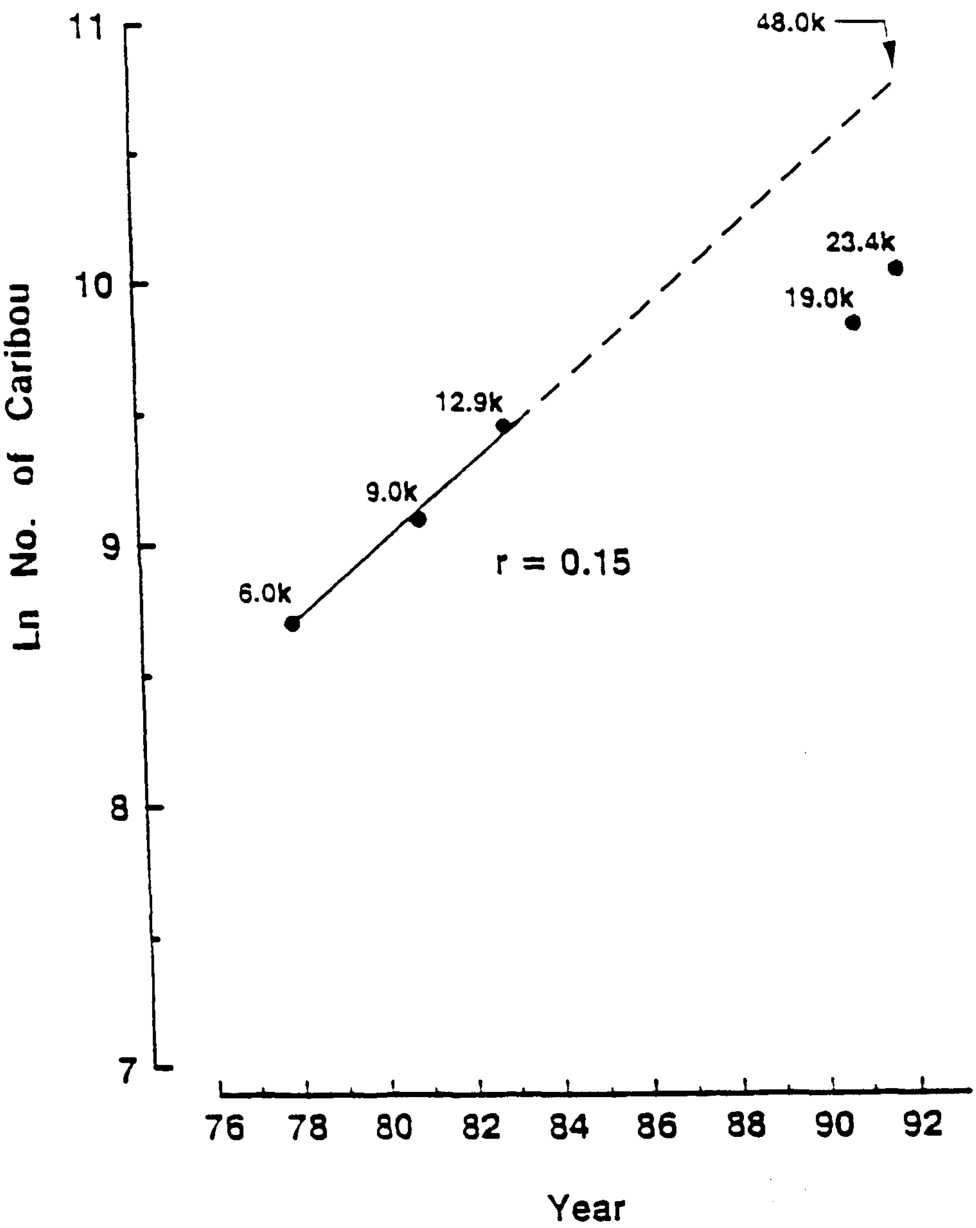

Fig. 1. Growth of the Central Arctic Caribou Herd, 1978-92. Census estimates by Whitten and Cameron (1983*b*), D. Reed (unpubl. data), and K. Whitten (unpubl. data). From Cameron (1993).

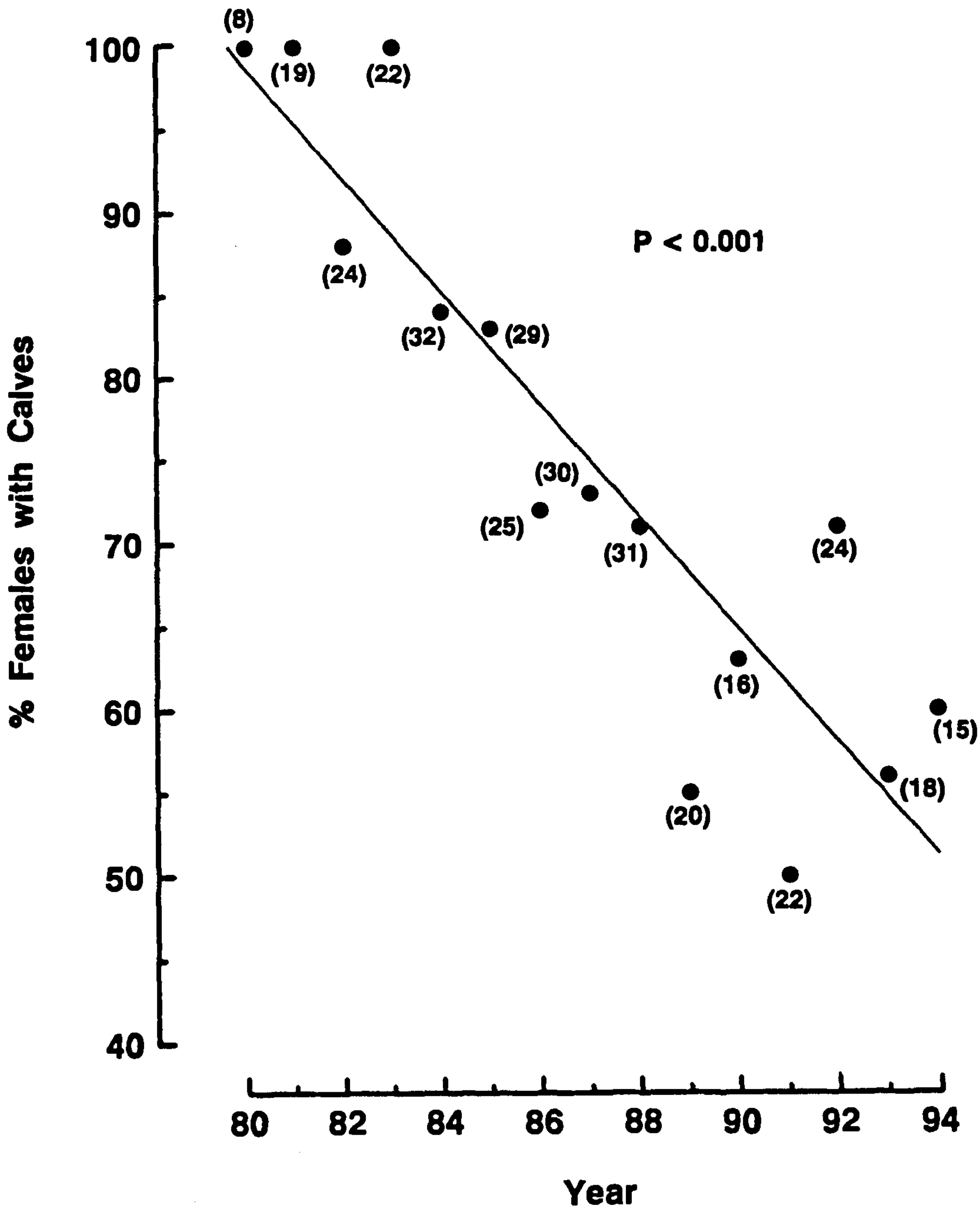

Fig. 2. Decline in calf production of the Central Arctic Caribou Herd, 1980-93. Estimates based on observations of radiocollared adult (i.e., sexually mature) females (n) from 10 June through 15 August. Note: Data not adjusted for east-west differences in herd productivity. Adapted from Cameron (1993).

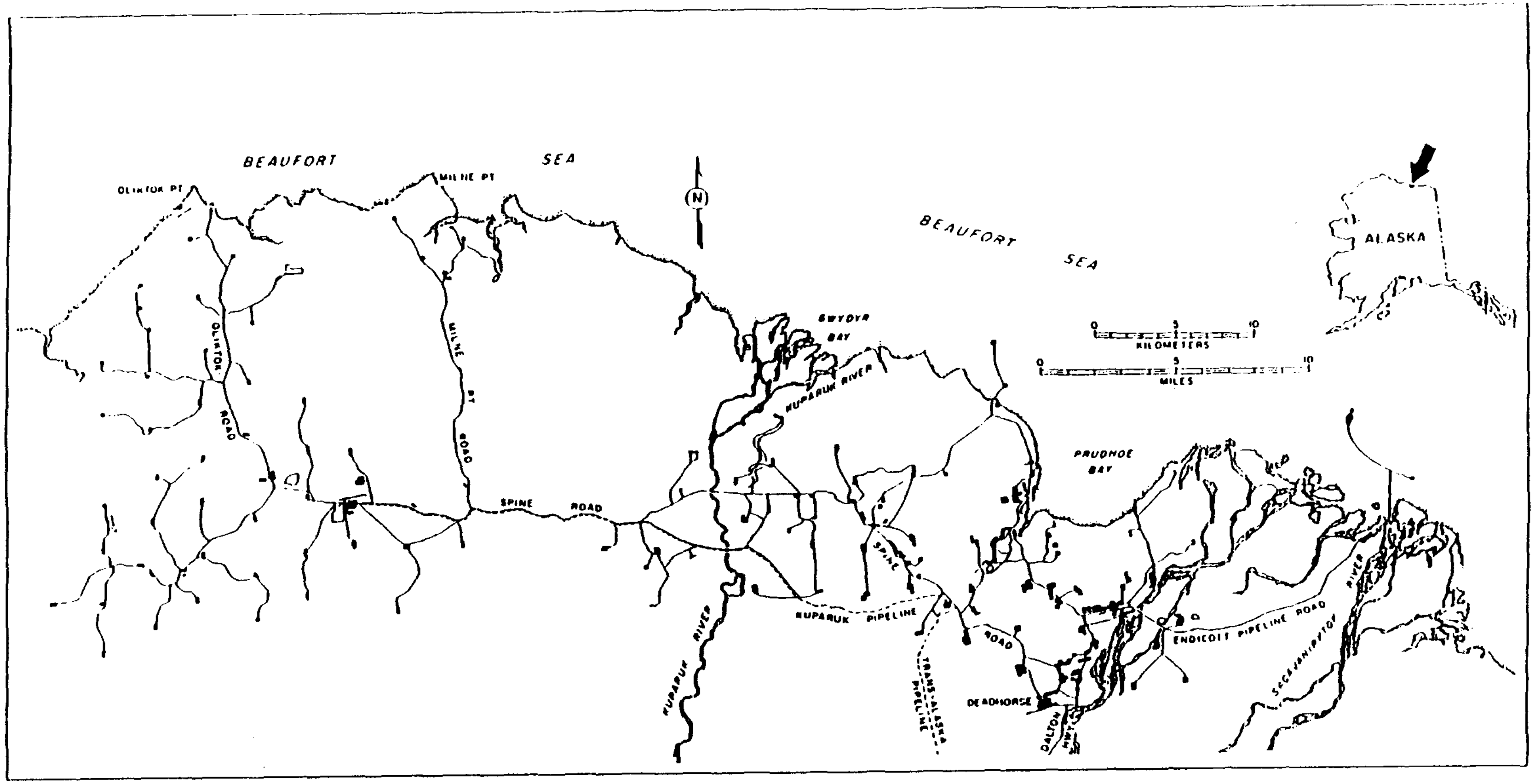

Fig. 3. Development in the Prudhoe Bay region. Alaska, ca. 1990. From Cameron *et al*., in prep. (B.1., Appendix A).

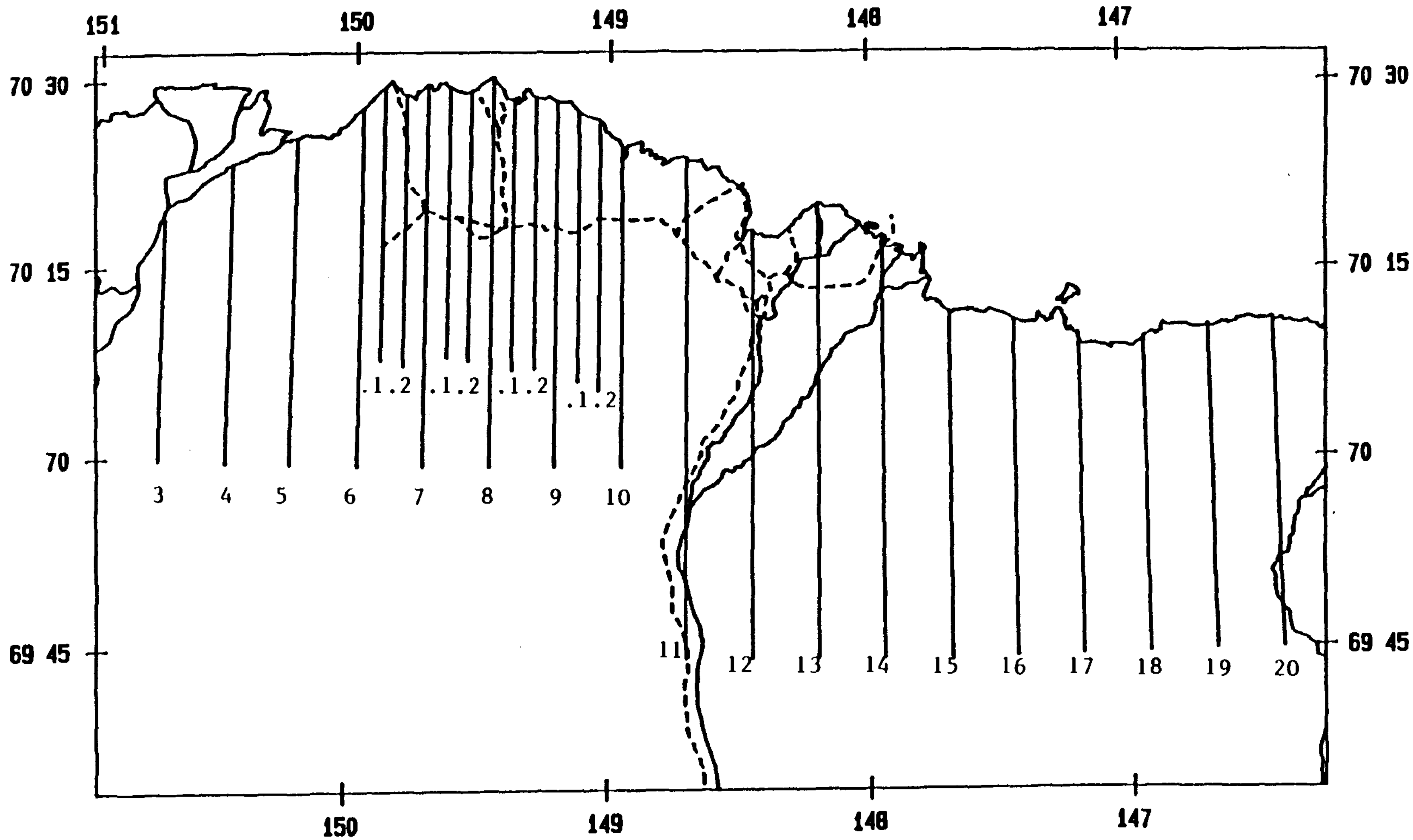

Fig. 4. Center lines of transects surveyed by helicopter during calving within the range of the Central Arctic Herd. From Smith and Cameron 1992.

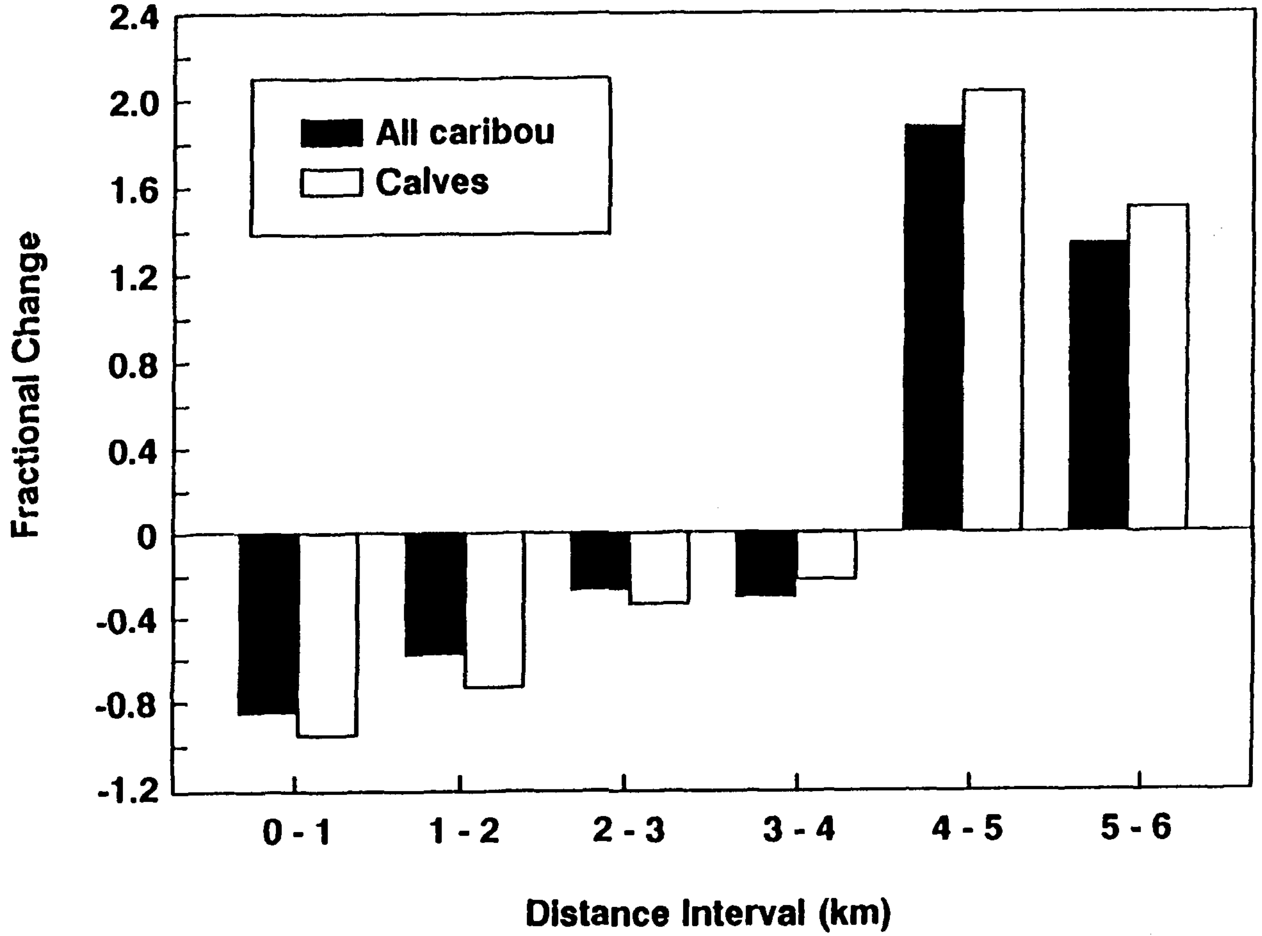

Fig. 5. Mean fractional changes in relative caribou abundance (i.e., percent distribution among strata, adjusted for differences in area) for 1 km distance intervals from the Milne Point road system, 1982-87 vs. 1978-81. From Cameron *et al.* (1992*a*).

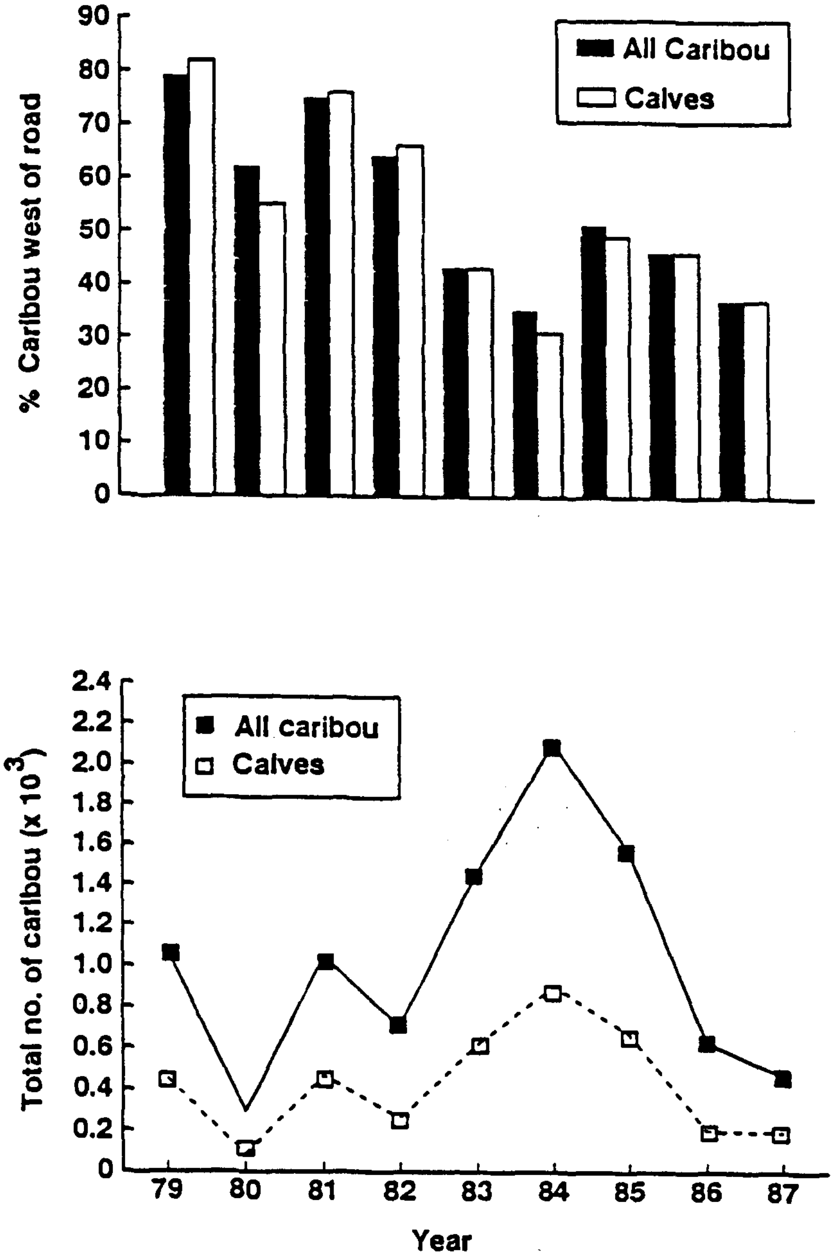

Fig. 6. Decline in percent abundance of caribou west of the Milne Point Road (Spearman's Rank, $P < 0.02$), and changes in total numbers of caribou observed north of the Spine Road (see Fig. 3, 1979-87. From Cameron *et al.* (1992*a*).

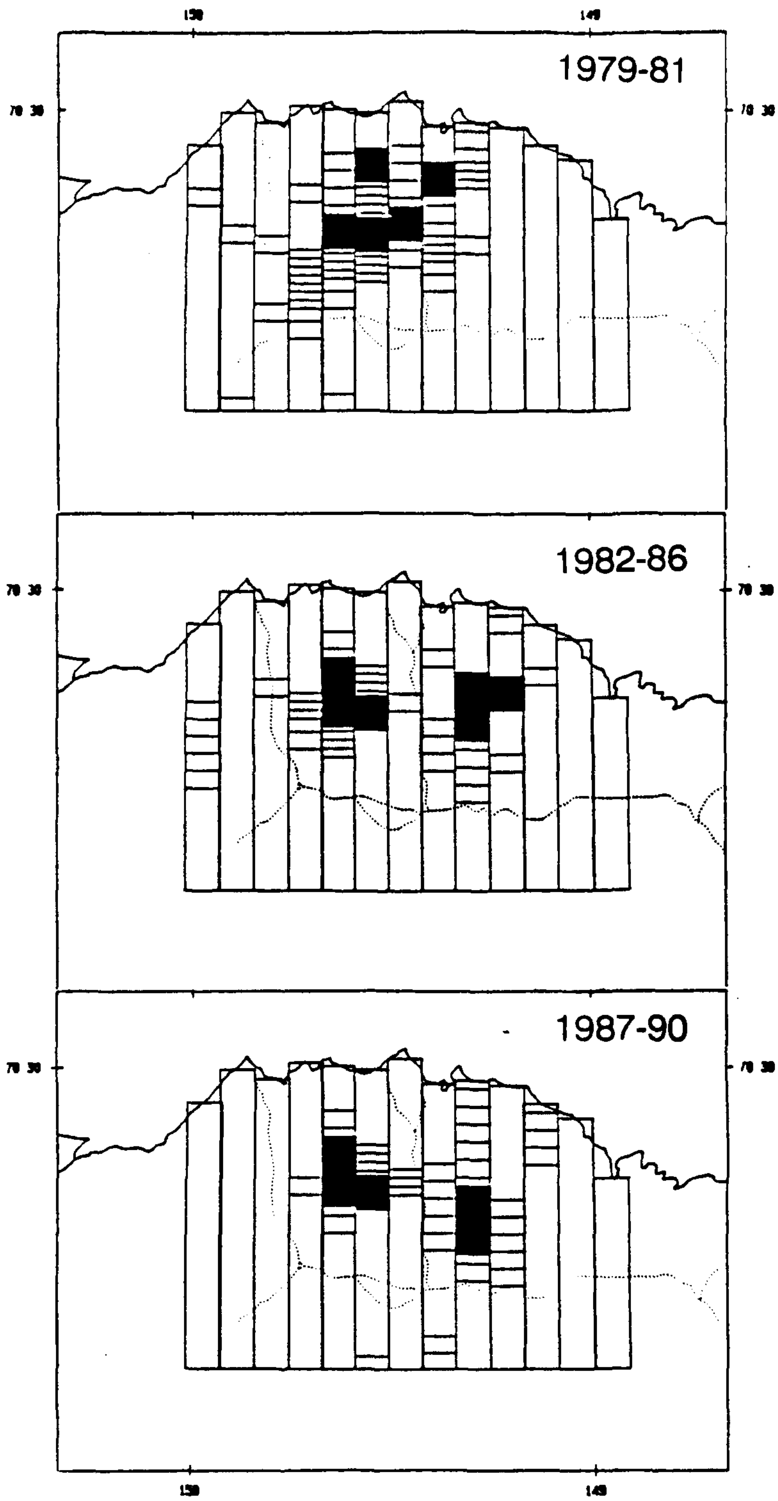

Fig. 7. Changes in mean relative distribution of Central Arctic Herd caribou in the Kuparuk Development Area during calving: 1979-81, 1982-86, and 1987-90. Shown only are those 10.4 km^2 transect segments in which the occurrence of caribou exceeded the area contribution to total coverage (0.9%). Gradations in line spacing depict multiples of observed use relative to availability: wide, <3X; narrow, >3X-5X; solid, >5X. From Smith and Cameron (1992).

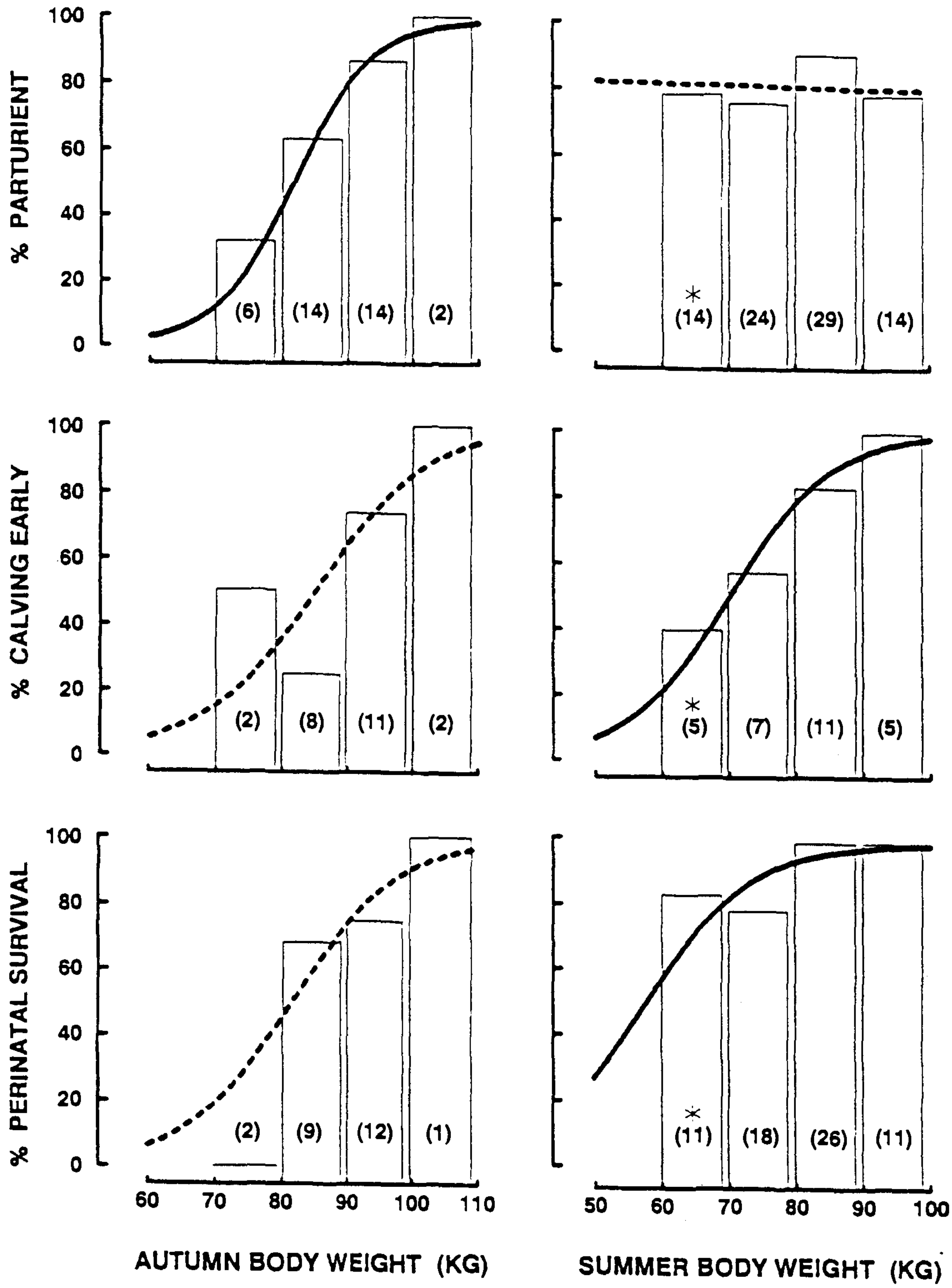

Fig. 8. Logistic regressions (solid lines are significant at $P < 0.05$) of parturition rate, incidence of early calving (i.e., on or before 7 June), and perinatal (>2 days post partum) calf survival on autumn and summer body weights of female caribou, Central Arctic Herd, 1987-1991. The empirical percentages 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. From Cameron *et al.* (1993).

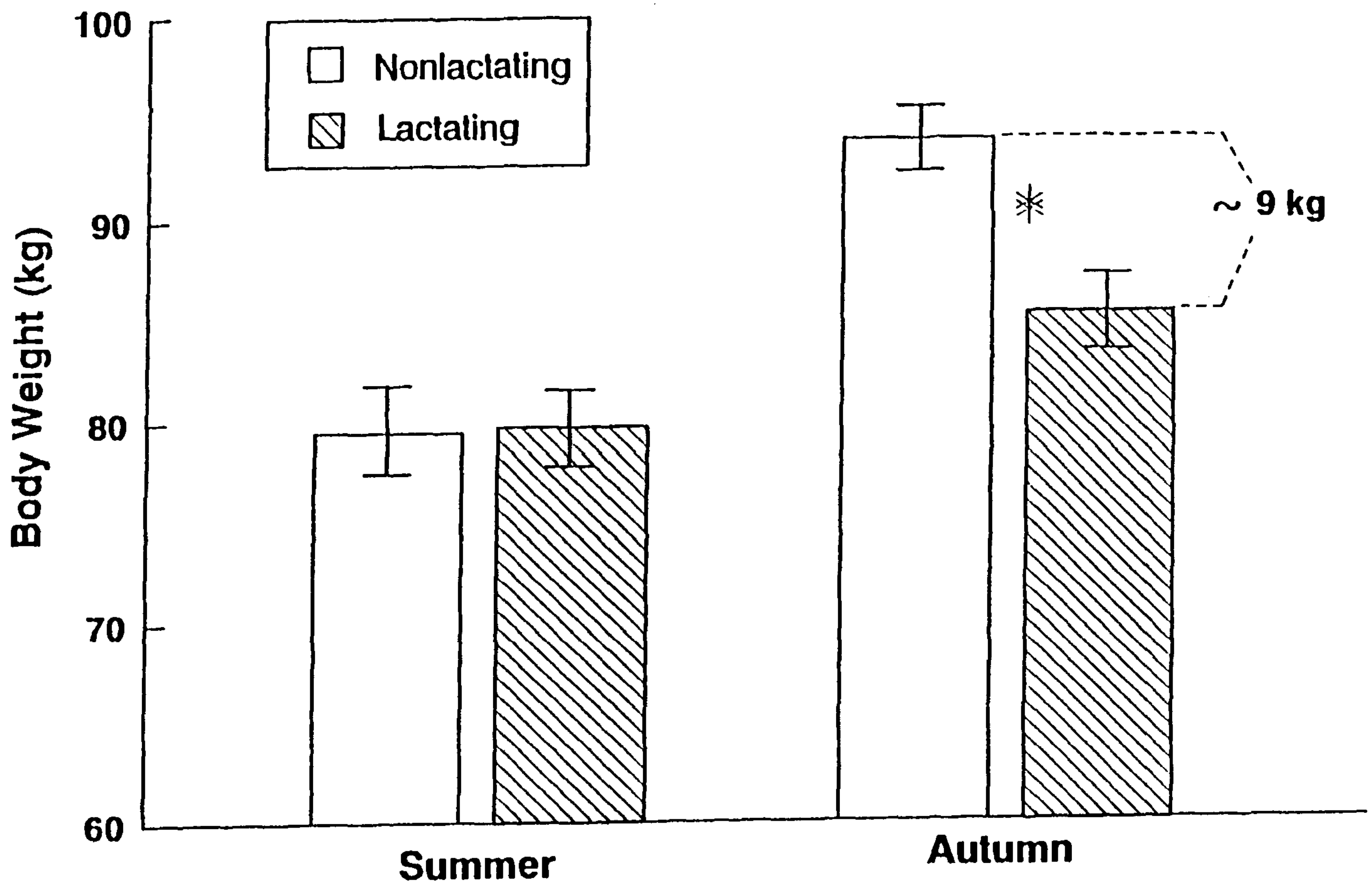

Fig. 9. Mean (± SE) body weights of lactating and nonlactating female caribou in summer (July) and autumn (October). From Cameron and White (1992). *Significant at $P < 0.001$.

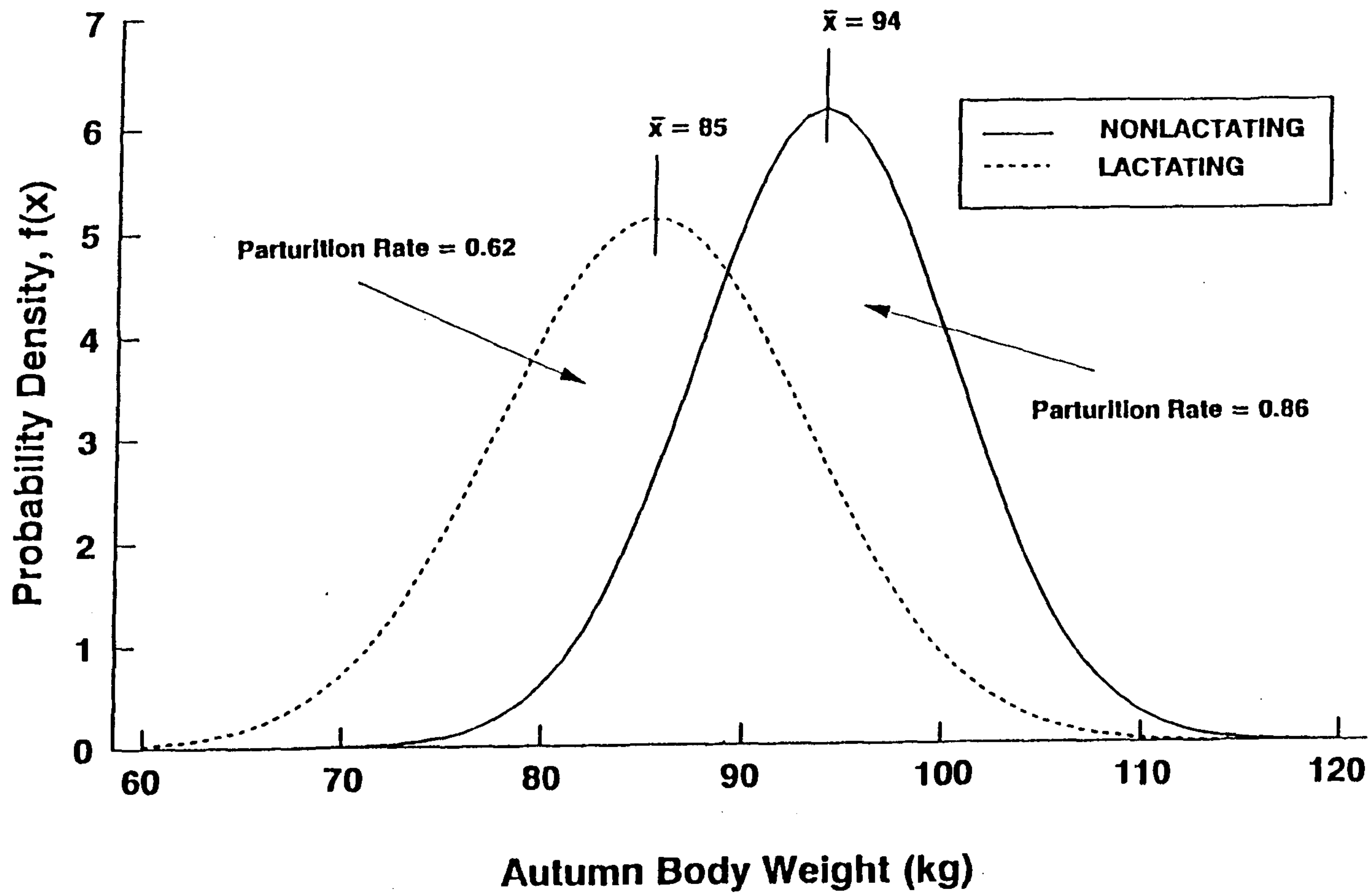

Fig. 10. Distributions of observed autumn (October) body weights for lactating and nonlactating female caribou. The associated parturition rates are integrated estimates derived from the logistic model (Fig. 8). From Cameron and White (1992).

Appendix A. Publication status, Study 3.35.

A. Published or In Press

1. Cameron, R. D., W. T. Smith, and R. T. Shideler. 1988. Variations in initial calf production of the Central Arctic caribou herd. Proc. Third North American Caribou Workshop. Alaska Dep. Fish and Game, Wildl. Tech. Bull. 8:1-7.

2. Cameron R. D., W. T. Smith, and S. G. Fancy. 1991. Comparative body weights of pregnant/lactating and nonpregnant female caribou. Pages 109-114 in C. E. Butler and S. P. Mahoney, eds. Proc. Fourth North American Caribou Workshop. Newfoundland and Labrador Wildl. Div., St. John's.

3. Cameron, R. D., D. J. Reed, J. R. Dau, and W. T. Smith. 1992. Redistribution of caribou in response to oilfield development on the Arctic Slope of Alaska. Arctic. 45:338-342.

4. Cameron, R. D., W. T. Smith, S. G. Fancy, K. L. Gerhart, and R. G. White. 1993. Calving success of female caribou in relation to body weight. Can. J. Zool. 71:480-486.

5. Cameron, R. D. 1994. Reproductive pauses by female caribou. J. Mamm. 75:10-13.

6. Cameron, R. D., and D. B. Stone. 1994. To weigh or to mass, the question is in the balance. Wildl. Soc. Bull. 22(3):In press.

7. Smith, W. T., R. D. Cameron, and D. J. Reed. 1994. Distribution and movements of caribou in relation to roads and pipelines, Kuparuk Development Area, 1978-90. Alaska Dep. Fish and Game, Wildl. Tech. Bull. 12. 54pp.

8. Cameron, R. D., and J. M. Ver Hoef. 1994. Predicting parturition rate of caribou from autumn body mass. J. Wildl. Manage. 58:674-679.

B. In Preparation

1. Cameron, R. D., E. A. Lenart, D. J. Reed, K. R. Whitten, and W. T. Smith. Abundance and movements of caribou in the oilfield complex near Prudhoe Bay, Alaska. For Rangifer (submitted 8/94).

2. Cameron, R. D., and R. G. White. Compensatory weight changes in free-ranging caribou. For Comp. Biochem. Physiol. A.

3. Griffith, B., and R. D. Cameron. Calving distribution of the Central Arctic and Porcupine caribou herds. For Arctic.

4. Cameron, R. D., J. M. Ver Hoef, and S. C. Bishop. Habitat selection by calving caribou of the Central Arctic Herd, Alaska. For Arctic Alpine Res.

5. Cameron, R. D., and R. T. Bowyer. Density-dependent responses by arctic caribou. For Oikos.

6. Nellemann, C., and R. D. Cameron. Terrain preferences of calving caribou exposed to oil development. For Arctic.

7. Gerhart, K. L., R. G. White, R. D. Cameron, and D. E. Russell. Body growth and chemical composition of arctic caribou from birth to maturity. For Can. J. Zool.

8. Gerhart, K. L., D. E. Russell, D. Wetering, R. G. White, and R. D. Cameron. Pregnancy in caribou: effects of body condition and lactation. For J. Zool. London.

9. Smith, M. D., and R. D. Cameron. Coastal-inland differences in caribou summer habitat on the Arctic Coastal Plain. For Arctic Alpine Res.

10. Cameron, R. D. Can petroleum development depress the productivity of arctic caribou? For Proc. Second Arctic Ungulate Conf., University of Alaska Fairbanks, August 1995.

Appendix B. Manuscript published in *Journal of Wildlife Management* 58:674-679 (1994).

PREDICTING PARTURITION RATE OF CARIBOU FROM AUTUMN BODY MASS

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Abstract: Body condition indices are potentially useful as predictors of fecundity in ungulates. We updated a logistic-regression model of the relationship between probability of parturition for adult caribou (Rangifer tarandus) and body mass during the previous autumn (model significance, $P = 0.025$). We also derived a model for herd parturition rate on the basis of the logistic regression for individual females and the mean and standard deviation of body mass. Small shifts in mass 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 representative masses for a herd when attempting to make predictions. Because of 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 or through systematic counts of newborn calves, antlers, and udders.

Key words: Alaska, body mass, body weight, calving, caribou, fecundity, logistic regression, model, parturition, Rangifer tarandus, reproduction.

Recent studies of barren-ground caribou in northern Alaska showed that the probability of parturition for adult (i.e., sexually mature) females varies with body mass (or weight; Cameron and Stone 1994) during the previous autumn (i.e., an index of pre-rut body condition), whereas calving date and perinatal calf survival are more closely related to mass in early summer (i.e., an index of condition during late gestation) (Cameron et al. 1993). These findings corroborated previous evidence for caribou that the probability of conceiving and carrying a fetus to term is determined primarily by summer nutrition (Dauphine 1976, Reimers 1983, Eloranta and Nieminen 1986), in contrast to the timing of parturition and early survival of offspring, which are more closely linked to winter nutrition (Espmark 1980; Rognmo et al. 1983; Skogland 1983, 1984; Eloranta and Nieminen 1986; Adamczewski et al. 1987).

Carryover effects between seasons could obscure this distinction. Nutrient insufficiency during summer, by reducing the body mass achieved by autumn, may reinforce the tendency for overwinter mass loss. Similarly, winter undernutrition, by depressing postpartum mass, may compromise mass gains in summer. Superior foraging conditions, however, should tend to either compensate for previous undernutrition or buffer the effects of subsequent undernutrition. Logically, successive favorable or unfavorable seasons would accelerate enhancement or deterioration, respectively, of body condition.

Superimposed on a variable intake of forage are the metabolic requirements of gestation and lactation. If a female caribou repeatedly fails to compensate for costs of reproduction, autumn body mass eventually will deteriorate to the point that she will undergo a breeding pause, followed by a recovery in condition and resumed reproduction 1 year later (Dauphine 1976, Reimers 1983, Cameron 1994). Because pauses are generally asynchronous, several subdistributions of mass for adult females will be present in the herd during a particular year, each representing a different phase of the cycle, and not all will pause with exactly the same frequency (Cameron 1994). Nonetheless, a measure of overall condition of those females in autumn is the distribution of their body masses, from which a subsequent parturition rate can be projected using an appropriate mathematical model. If, in addition, the nonfecund status of subadult (i.e., sexually immature) females is consistent with that same model, estimating a herd-level rate of parturition should be possible.

We update a published relationship (Cameron et al. 1993) between probability of parturition and autumn body mass of adult female caribou. We also derive a model for predicting herd parturition rate and discuss its use as a management tool.

The study was supported by Federal Aid in Wildlife Restoration and the Alaska Department of Fish and Game, Division of Wildlife Conservation. We are grateful to E. F. Becker, K. L. Gerhart, E. A. Lenart, L. A. McCarthy, and K. R. Whitten for technical assistance. R. T. Bowyer, K. L. Gerhart, D. J. Reed, R. G. White, and 2 anonymous referees commented on a draft manuscript.

METHODS

On 3-9 October 1991, we immobilized, radio-collared (as necessary), and weighed (nearest 1 kg) (Cameron et al. 1993) 15 adult female caribou of the Central Arctic Herd (Cameron and Whitten 1979). We relocated and observed radio-collared caribou every 1-3 days by fixed-wing aircraft during 6-12 June 1992. We determined parturition status from presence of a calf, antler retention, and udder distension (Whitten et al. 1992, Cameron et al. 1993). If we observed females with newborn calves, hard antlers, or developed udders, we considered them parturient. We classified females consistently lacking those characteristics as nonparturient.

Using $\underline{t}$-tests, we compared mean body mass for parturient and nonparturient females. We used logistic regression (Hosmer and Lemeshow 1989) to model the probability of pregnancy as a function of body mass during the previous autumn. The logistic model is

$$p(x;\beta_0,\beta_1) = \frac{e^{\beta_0 + \beta_1 x}}{1 + e^{\beta_0 + \beta_1 x}}, \qquad (1)$$

where $p(x;\beta_0,\beta_1)$ is the probability of parturition, x is autumn body mass, and β_0 and β_1 are parameters. Cameron et al. (1993:482) estimated the parameters to be $\hat{\beta}_0 = -15.562$ and $\hat{\beta}_1 = 0.190$. In all cases, we used $\alpha = 0.05$.

We examined a more general model by considering body mass and year. We began with a full model, including interactions, and discarded terms on the basis of score tests (Hosmer and Lemeshow 1989:16), P-to-remove at 0.05, using exact logistic regression (CYTEL Software Corp. 1993). In this manner, we attempted to update, with 1991-92 data, the specific model of equation (1) reported previously (Cameron et al. 1993). We assessed goodness-of-fit from Pearson and deviance residuals (Hosmer and Lemeshow 1989:137). We used maximum likelihood to obtain final parameter estimates (SAS Inst. Inc. 1990).

To estimate herd parturition rate, it is necessary to average the parturition probabilities for all females in a sample. This may be modeled by assigning a continuous distribution $f(x)$ to mass that represents the relative numbers of individuals at mass x, where $f(x)$ is normalized:

$$\int_{-\infty}^{\infty} f(x)dx = 1.$$

For example, let $f(x;\mu,\sigma)$ be a normal distribution with 2 parameters, the mean μ and standard deviation σ. The expected number of females in any mass class between masses a and $a + \Delta$ is

$$N \int_{a}^{a+\Delta} f(x;\mu,\sigma)dx ,$$

where N is the population of those females. Then expected parturition rate is

$$\pi(\beta_0,\beta_1,\mu,\sigma) = \int_{-\infty}^{\infty} p(x;\beta_0,\beta_1) f(x;\mu,\sigma)dx , \qquad (2)$$

where $p(x;\beta_0,\beta_1)$ is the logistic regression for individual females (equation 1). Herd parturition rate varies with the logistic-regression parameters β_0 and β_1 and the normal-distribution parameters μ and σ. Equation (2) was used to examine the sensitivity of parturition rate to changes in parameters describing the mass distribution.

RESULTS

Determinations of parturition status in 1992 were unambiguous, despite the comparative lateness of surveys. Of 15 female caribou radio-tracked, we observed 11 with calves at heel. All 4 of the remaining females had shed their hard antlers when first located early in the survey period, and new velvet growth was evident; none had distended udders.

Fifty-one adult female caribou of the Central Arctic Herd have been weighed in autumn and then relocated and observed the following June (Table 1). Yearly samples were small, and in only 2 of 5 years did mean mass of parturient and nonparturient females differ. Pooled means, however, were different.

In logistic-regression modeling of parturition probability, year and its interaction with body mass were removed (score tests, $\underline{P}$ = 0.583 and 0.083, respectively). The resultant model included only autumn body mass ($\underline{P}$ of β_1 = 0.025; Fig. 1). Pearson and deviance residuals did not show lack of fit for the final model ($\underline{P}$ > 0.5).

A model of parturition rates for adult females in the herd was generated from equation (2), incorporating the updated logistic regression (Fig. 1), and plotted as a response surface for various combinations of means and standard deviations of body mass. The herd model (Fig. 2) shows that, although parturition rate increases with mean mass over a wide range, sensitivity (i.e., instantaneous rate of change) varies with parameters of mass distribution. At small standard deviations, minor changes in mean body mass are associated with major changes in parturition rate, but as standard deviation increases, the function approaches linearity and flattens, and the same changes in mean mass effect progressively smaller changes in parturition rate.

DISCUSSION

Retaining a year effect and its interaction with autumn body mass in the logistic-regression model would be equivalent to having several annual models, each based only on mass. Although no year effects were detectable, we cannot discount that possibility because sample sizes were small (Table 1). Hence, it is best to view the response variable of the updated model (Fig. 1) as an average, across-years estimate of parturition probability. Within the limits of our observations, however, this model accommodates disparate years. In fact, yearly models, if indicated, would be useless for prediction.

Adding the 1991-92 data changed the shape of the logistic regression, indicating that mass may not be adequate as an explanatory variable for parturition status. Other indices of body condition (e.g., fat content; Thomas 1982, Crête et al. 1993) may be superior, but individual differences in reproductive capability within condition classes probably would render any predictor imperfect.

Surprisingly, metatarsal lengths, obtained for a subset of 40 females, were of no value as covariates. The metatarsus, which attains adult length within 2 years (Dauphine 1976), should be a reasonable reference for skeletal size and, consequently, useful for scaling body mass. At similar autumn masses, small females should be in better condition than large females and, therefore, more likely to become pregnant (Albon et al. 1986). If not generally applicable within herds, a body size index may improve among-herd models, for example, those describing caribou in the Arctic and their larger-bodied counterparts in interior and southwestern Alaska.

According to our herd model (Fig. 2), parturition rate is sensitive to changes in mass distribution of adult females, particularly when data overlie the steepest portion of the logistic-regression curve. Given a standard deviation of 8, which approximates that of our overall sample (Table 1), a 6% mean decrease in body mass (from 85 to 80 kg) equates to a projected 17% decline in parturition rate (from 0.63 to 0.52). Such disproportionate changes in parturition rate underscore the importance of multiplier effects in forage quality and availability on autumn mass (White 1983).

Conversely, shifts in parturition rate are associated with relatively smaller changes in mean body mass, a consequence of the mechanism by which parturition status of individuals is altered. Rather than continuing to deteriorate in condition beyond when they fail to become pregnant, adult females gain mass because reproductive demands are absent. That recovery virtually ensures conception the next year, followed by a decline in mass each year, on average, with successive pregnancy and lactation bouts until a lower critical mass is again reached, and another pause occurs (Fig. 3). A declining trend in parturition rate occurs with reduced mass gains during pause years and accelerated losses thereafter. Pause cycles are progressively abbreviated, yielding increasing numbers of nonbreeding females. Because the latter subsequently recycle in body mass, however, the decline in mean mass of adult females in the herd lags behind the downward shift in parturition rate. Incidentally, any increase in the proportion of nonbreeders represents an equivalent increase in pause frequency, the mathematical complement of parturition rate.

Because any change in mean body mass of adult females is small relative to the corresponding change in parturition rate, sampling a herd becomes problematic. To restate the example above, one must be capable of detecting a 5-kg decline in mean mass to confidently predict an 11-unit decrease in parturition rate.

Fecundity of subadults in a herd, although highly variable, is consistent with mass criteria for adults. Yearlings and 2 year olds in the Arctic tend to be reproductively inactive (Whitten 1991), but those in interior Alaska may breed under favorable circumstances (Davis et al. 1991), suggesting a condition-dependent, and therefore age-independent, relationship (Reimers 1983, Cameron et al. 1993). If body mass applies to all age classes as a condition index, nonparturient status would be predicted appropriately for most subadults in arctic herds, but the additional mass categories would contribute further to sampling difficulties.

For herds in which fecundity of adult females is consistently high (i.e., >90%), parturition rate varies inversely with the proportion of nulliparous 2 year olds present (Bergerud 1971). Under exceptional foraging conditions, calf production is augmented further by subadult pregnancies (Davis et al. 1991). High productivity tends to persist because most adult females remain in high mass classes (Fig. 3) and, therefore, are affected little by environmental extremes that depress nutritional status. This mass reserve may explain the higher tolerance of some herds for the periodic adverse effects of weather on forage quality, insect activity, or snow depth. Nevertheless, sustained nutrient insufficiency, be it weather induced or a consequence of increasing caribou density, will produce a downward trend in female masses, with an accelerating decline in parturition rate.

Calf mortality also has a stabilizing effect on body mass distribution of adult females and, therefore, on parturition rate. Whether calf loss occurs early (i.e., before or during peak lactation) or late in summer (i.e., after peak lactation, but before weaning), affected females would gain more mass by autumn than their fully lactating counterparts, thereby increasing the likelihood of conceiving that year and delaying the next reproductive pause.

MANAGEMENT IMPLICATIONS

An important, but generally unrecognized, mechanism by which parturition rate of a herd may change is through a shift in the mean frequency of reproductive pauses by adult females. In turn, pause frequency varies with the distribution of body mass, which is resistant to change because of feedback from the cyclic process that it influences.

This complex interdependency of variables pertaining to adult females, together with a changing presence of subadult females, limits the use of our model as a predictive tool. In addition to high costs of capture, obtaining representative masses for a herd is difficult, and biased samples will generate erroneous predictions. In particular, detecting or forecasting density-dependent changes in parturition rate by monitoring body mass may not be possible. For routine estimates of parturition rate, we recommend directly determining reproductive success of radio-collared females (Whitten et al. 1992) or systematic counts of calves, retained antlers, and distended udders early in the calving period (K. R. Whitten, Alas. Dep. Fish and Game, Fairbanks, unpubl. data).

Any mortality of nursing calves, because of a positive influence on subsequent fecundity of their dams (Davis et al. 1991), must be considered when assessing observed changes in herd parturition rate. Equally crucial is determining the cause of that mortality. High perinatal losses, principally a result of undernutrition during late gestation (Rognmo et al. 1983, Skogland 1984, Eloranta and Nieminen 1986, Adamczewski et al. 1987, Cameron et al. 1993), might be incorrectly attributed to predation. Similarly, predation on newborn calves (Miller et al. 1985) could obscure nutritional stress if high pregnancy or parturition rates persist. Under either scenario, actions taken to reduce predation might actually exacerbate an existing problem related to chronic food limitation.

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Received 14 February 1993.
Accepted ________.
Associate Editor: White.

Table 1. Mean body mass of parturient and nonparturient adult[a] female caribou in autumn, Central Arctic Herd, Alaska, 1987-91.

	Body mass (kg)						
	Parturient[b]			Nonparturient			
Year	$\bar{x}$	SD	n	$\bar{x}$	SD	n	P^c
1987	87.1	5.6	9	83.5	8.2	4	0.370
1988	88.2	3.8	6	77.0	4.4	3	0.005
1989	92.5	5.2	8	81.0	7.1	2	0.030
1990	98.5	10.6	2	90.0	4.2	2	0.400
1991	93.2	11.5	11	91.8	3.8	4	0.810
1987-91	91.0	8.1	36	84.9	7.6	15	0.017

[a] All were sexually mature, on the basis of current, or previously observed pregnancy.
[b] Based on observations during the following Jun.
[c] *t*-test.

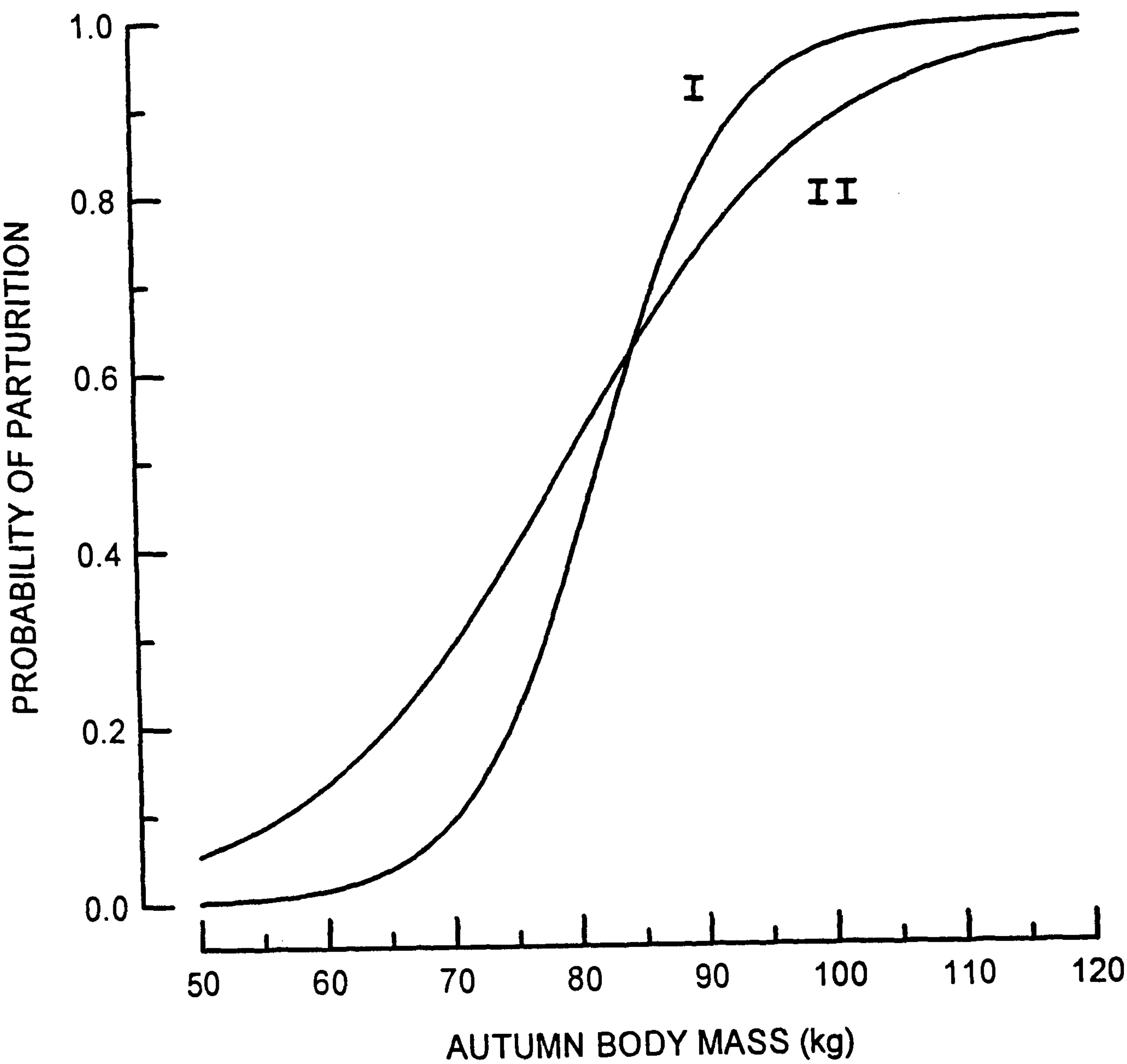

Fig. 1. Logistic regressions (equation 1) relating probability of parturition for adult female caribou to autumn body mass, Central Arctic Herd, Alaska, 1987-92. Model I ($\hat{\beta}_0$ = -15.562, $\hat{\beta}_1$ = 0.190; $\underline{P} < 0.01$ is from Cameron et al. (1993). Model II ($\hat{\beta}_0$ = -7.690, $\hat{\beta}_1$ = 0.097; $\underline{P} = 0.025$) is the updated version incorporating data from 1991-92.

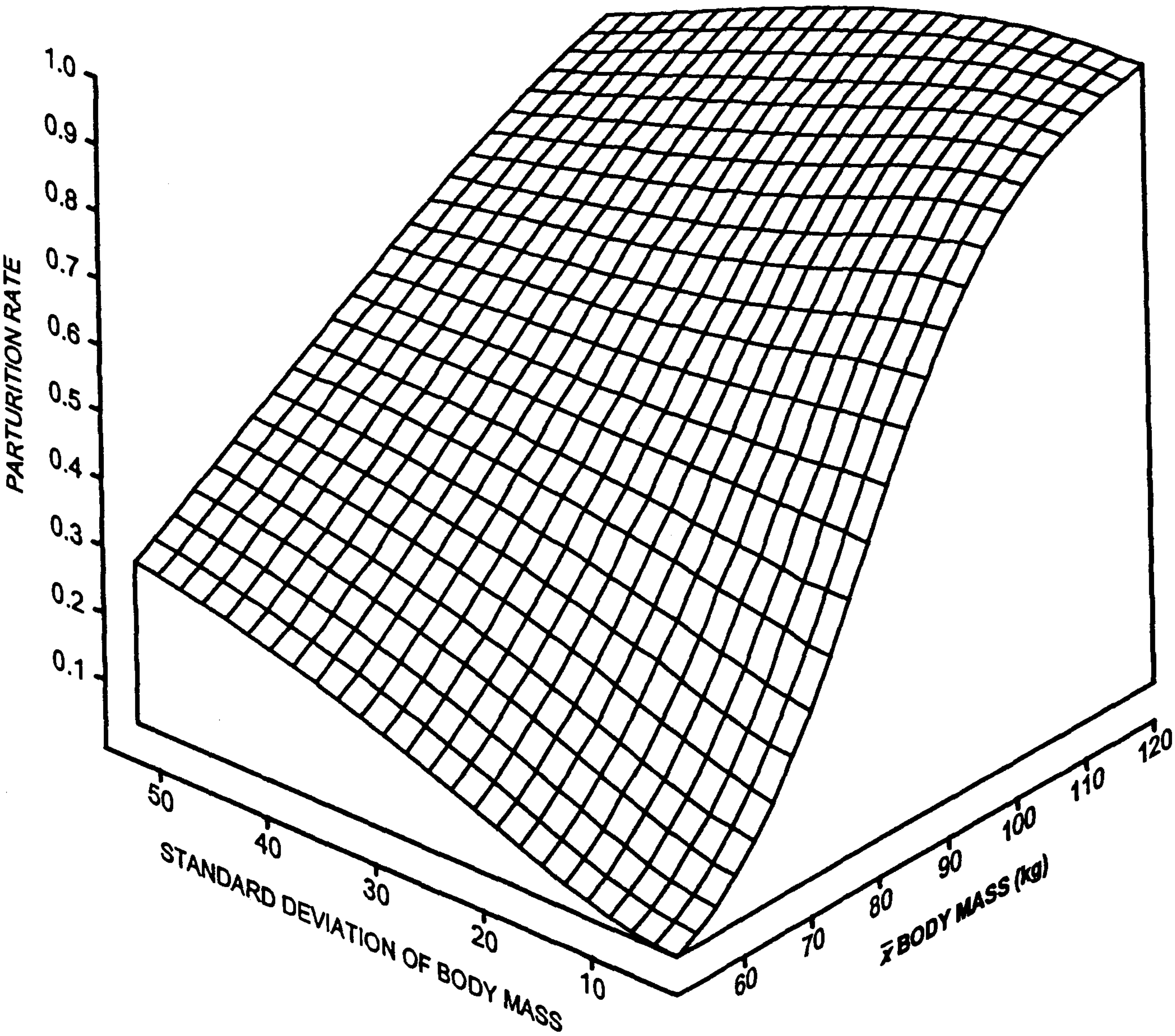

Fig. 2 Response surface of parturition rate of the Central Arctic caribou herd, Alaska, in relation to mean ($\bar{x}$) and standard deviation (SD) of autumn body mass, 1987-92: π (-7.690, 0.097, $\bar{x}$, SD) (equation 2).

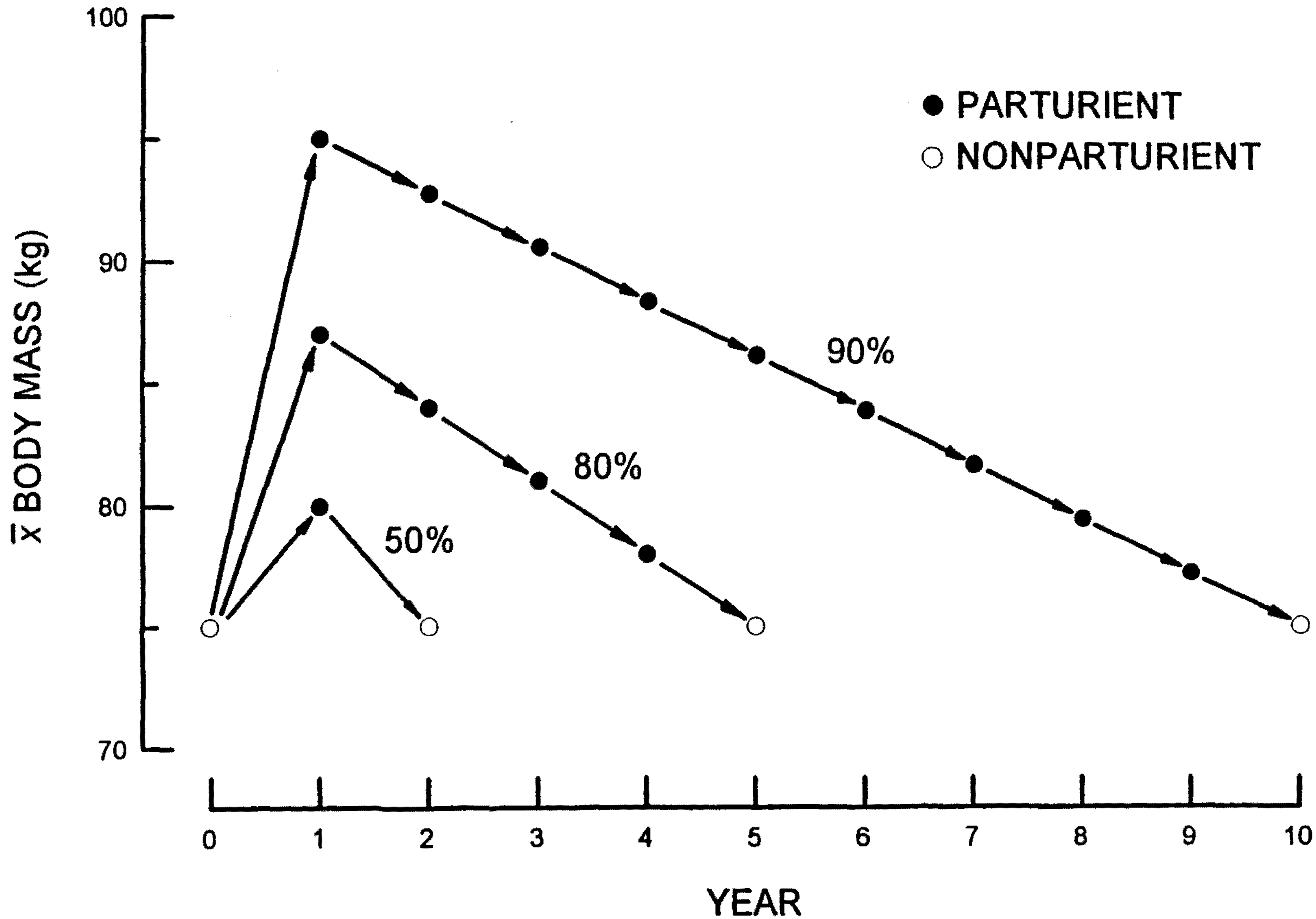

Fig. 3. Hypothetical changes in mean mass of adult female caribou in autumn at herd parturition rates of 50, 80, and 90% (i.e., reproductive pause frequencies of 50, 20, and 10%, respectively).

Appendix C. Abstract of manuscript submitted to *Rangifer*, August 1994.

Abundance and movements of caribou in the oilfield complex near Prudhoe Bay, Alaska

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Abstract: We examined the distribution and movements of 141 radio-collared female caribou (Rangifer tarandus granti) of the Central Arctic Herd during summer, 1980-93. Caribou locations within each of 5 quadrats along the arctic coast were totalled separately for days during which insects were active and inactive, and numbers of east-west crossings of each quadrat mid-line were determined from sequential observations. Both abundance and lateral movements of radio-collared females in the quadrat encompassing the intensively-developed Prudhoe Bay oilfield complex were significantly lower than in other quadrats ($P < 0.001$ and $P < 0.00001$, respectively). Avoidance of, and fewer movements within, the complex by female caribou are ostensibly in response to the dense network of production and support facilities, roads, above-ground pipelines, and the associated vehicular and human activity. Impaired access to this area constitutes a functional loss of habitat.

Appendix D. Manuscript to be published in *Wildlife Society Bulletin* 22.

TO WEIGH OR TO MASS, THE QUESTION IS IN THE BALANCE

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We are disturbed by the increasing -- and apparently arbitrary -- requirement to use "mass" as a substitute for "weight" when reporting the physical attributes of bodies, carcasses, and the like (e.g., Lancia 1990). The latter does the job rather nicely and is no less suitable than the former.

To review, "mass" refers to an absolute quantity of matter, which cannot be measured directly with any spring balance. Moreover, the term is not in general usage, even though the associated units, kilograms, are recognizable to almost everyone. What we do measure is a force known as "weight", defined as the product of mass and the acceleration due to gravity, which varies with location on the earth's surface. While the "weight" designation is familiar, its formal units, Newtons, are not; hence, the calibration of balances in kilograms using a somewhat arbitrary correction for gravity. Confusion over terminology presumably arises from earlier use of kilograms-weight as the unit of force (Smith 1949) (equivalent to the recently-defined Newton) that was loosely converted to kilograms of mass via an unspecified value for acceleration.

On the one hand, then, we have a term that describes what we don't measure, bound to units we've grown to accept; and, on the other, a correct term, insofar as it acknowledges spatial variability, encumbered by units that are foreign to most people, including biologists.

Chardine's (1986) treatment of the subject is reasonably convincing and basically accurate. He argues that "mass" can be estimated by assuming a constant gravitational influence. Good point, but why bother? Small errors notwithstanding (maximum about 1% for latitudinal and altitudinal effects, Stacey 1992), is it reasonable to discard comfortable terminology when there is no entirely acceptable substitute? We maintain that change is warranted only to enhance accuracy or clarity. Neither benefit applies here.

Logically and grammatically, we "weigh" various objects to obtain, not "masses", but "weights". Were it otherwise, those same objects would need to be "massed". Undesirable 'verbing' of nouns aside, we're both too old to change that much.

Total accuracy, even if it pertained to this micro-debate, is not everything. In a confusing world of slang and idioms, the familiar has value. Let's stay with "weight" or, at the very least, defer to author discretion. After all, the units do speak for themselves, and confusion is virtually impossible. To modify a well-worn adage, "Read what is meant, not necessarily what is written".

ACKNOWLEDGMENTS

E. E. Reed, proprietor of the Golden Eagle Saloon, provided the scholastic environment in which this note was conceived and nurtured. W. K. Witte critically reviewed the manuscript.

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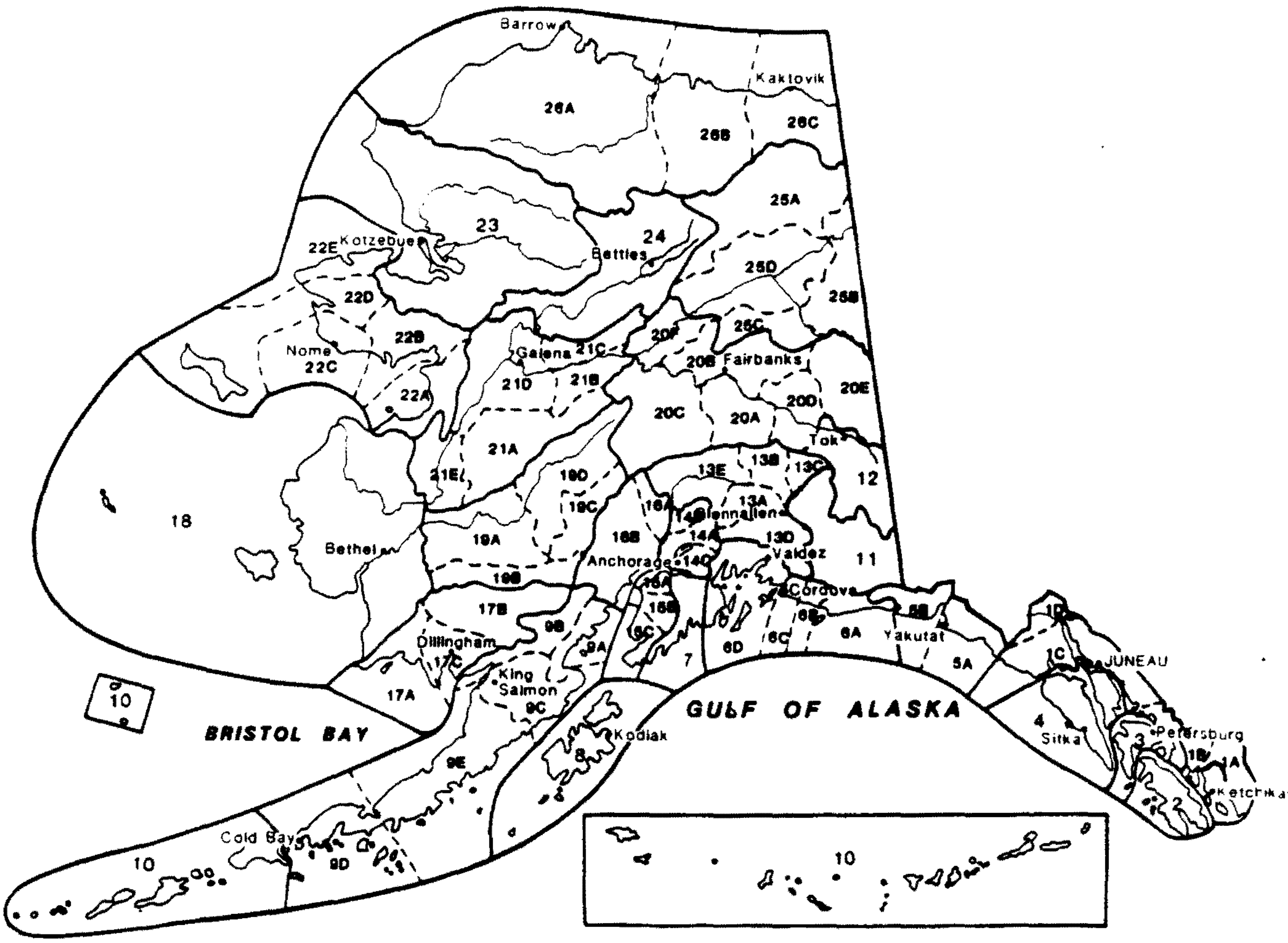
Alaska's Game Management Units



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.