Lactation in yearling Alaskan reindeer: Implications for growth, reproduction, and survival

Alexander K. Prichard, Greg L. Finstad & Drew H. Shain

Reindeer Research Program, School of Agriculture and Land Resources Management, 303 O'Neill Building, Univ. of Alaska Fairbanks, P.O.Box 757200, Fairbanks, AK 99775-7200, USA (fyrrp@uaf.edu).

Abstract: Unlike most *Rangifer* herds, free-ranging female reindeer (*Rangifer tarandus*) on the Seward Peninsula, Alaska frequently give birth as yearlings (12 months). In other reindeer herds this early reproduction has led to negative effects such as decreased future weight gain and reproduction. We analyzed reindeer data collected on the Seward Peninsula between 1987 and 1997 to determine what effect lactating as yearlings had on future weight gain, reproductive rates, and survival. Reindeer were rounded up during June and early July. Individual ear tag numbers were recorded, females were visually inspected for the presence of a distended udder, and some animals were weighed. Females with distended udders as yearlings had subsequent recapture rates, survival rates, weight gain, and future reproductive success comparable to females that did not have distended udders as yearlings. These findings suggest that the beneficial effects of increased calf weight gain outweigh potential negative effects of early reproduction in these reindeer. This may be due to high quality range leading to heavy calves and the ability of females to maintain body reserves during lactation.

Key words: *Rangifer tarandus,* life history, primiparity.

Rangifer, 19 (2): 77–84

Introduction

Age of first reproduction can have a strong influence on lifetime reproductive success and population growth in a species (Bell, 1980; Festa-Bianchet *et al.,* 1995). However, the high energetic costs of pregnancy and lactation may decrease fat and protein reserves leading to lower future survival and reproduction (Clutton-Brock *et al.,* 1983; Gerhart *et al.,* 1997). Past studies have suggested that the costs of early reproduction in *Rangifer* may include decreased maximum adult body weight, and decreased calf survival (Reimers, 1972; Lenvik & Aune, 1988; Ropstad *et al,* 1991), as well as decreased future reproductive output. Reimers (1983) found that two-year-old female reindeer that calved as yearlings had lower pregnancy rates than expected by body weight alone. Early primiparity also has been shown to decrease future weight gain in bighorn sheep (*Ovis canadensis;* Festa-Bianchet *et al,* 1995), and bison (*Bison bison;* Green & Rothstein, 1991). Festa-Bianchet et al. (1995) reported that bighorn sheep females that reproduced at two years of age had similar survival rates to age three, similar lactation rates as three year olds, but lower weight gain at age four than ewes that did not give birth as two year olds.

Reindeer and caribou (*Rangifer tarandus*) typically give birth for the first time at two years of age

(Skjenneberg & Slagsvold, 1968; Dauphiné, 1976; Reimers, 1997). Numerous studies have shown that the probability of reproducing in female reindeer and caribou is strongly correlated with body weight or fat reserves during the breeding season (Dauphiné, 1976; Thomas, 1982; Reimers, 1983; Lenvik *et al.*, 1988; Cameron *et al.*, 1993; Gerhart, 1995). Thomas (1982) reported that only yearling (21 month) Peary caribou (*R. t. pearyi*) weighing more than 46 kg and with high fat reserves were pregnant; pregnancy rates dropped steeply with body weights less than 58 kg. Crête *et al.* (1993) found that all captive female caribou that ovulated had at least 7.2 kg of stored fat regardless of age.

In a few reindeer herds with high calf body weights, females become pregnant as calves and give birth their second summer (Reimers, 1972; 1983; Ropstad *et al.*, 1991). In North Ottadalen, Norway, 47% of yearling female reindeer were lactating (Reimers, 1972). Similarly, in South and North Ottadalen, 3 out of 4 reindeer calves were found to be pregnant their first winter (Reimers, 1983). A study in Norway found that 20% of 632 reindeer calves were pregnant in winter and females that reproduced as yearlings had lower weight gain the following year (Ropstad *et al.*, 1991). Reindeer calves on the Seward Peninsula, Alaska exhibit rapid summer weight gain compared with many Scandinavian reindeer herds and wild caribou herds in North America (unpubl. data) and also have high pregnancy rates as yearlings.

We hypothesized that the nutritional demands of calving as a yearling will decrease weight gain of lactating yearling females and the survival and reproductive rates of early reproducing females will be lower the following year. Also, early reproduction may decrease skeletal size and maximum body weight, further decreasing lifetime reproductive success and survival.

Study area

This study was conducted on the reindeer range of Mr. Lawrence Davis (Fig. 1), which consists of 3875 km² north of Nome, Alaska. Based on yearly handling records, the herd has increased in size from approximately 4000 in 1987 to approximately 8000 animals in 1997. Calving occurs in late April or early May (Chetkiewicz, 1993). Reindeer were handled in a corral located approximately 8 km north of Nome, Alaska (lat. 64°38'N long. 165°20'W). The average January temperature is -15 °C, the average July temperature is 10.3 °C. Average rainfall is 422 mm per year. Predators include wolves (*Canis lupus*), wolverines (*Gulo gulo*), red foxes (*Vulpes vulpes*), and brown bears (*Ursus arctos;* Chetkiewicz, 1993).

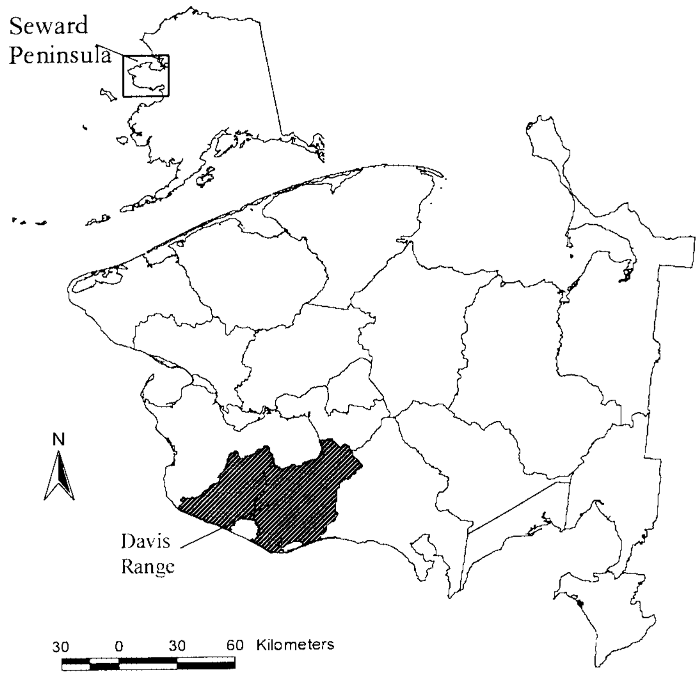

Fig. 1. The range of the Davis reindeer herd, north of Nome, Alaska.

Methods

Reindeer on the Seward Peninsula are owned and managed by individual Alaskan Natives or Native Corporations. Reindeer are free-ranging with no supplemental feeding and are rounded-up every June and July and herded into a corral. Animals are then handled individually. Groups of several hundred to 2500 reindeer are corralled at one time. Therefore, there are multiple corrallings each summer. Reindeer calves are given a numbered eartag, adults are vaccinated for brucellosis, antlers are harvested, some animals are weighed, and females are visually inspected for the presence of a distended udder (Bergerud, 1964). Reindeer were also handled in January during the years 1987 through 1991.

Female adult reindeer (>12 months; n = 781) were weighed between 1987 and 1997 when logistics and personnel allowed. Adult animals were weighed to the nearest 0.5 kg using a Numak® pneumatic animal crush mounted on Tru-test® load bars. Starting in 1987, 2876 female yearling reindeer were checked for a distended udder. There were 3458 recaptures of these females (> 24 months) that allowed us to check for subsequent reproduction based on the presence of a distended udder. All procedures for animal use have been reviewed and accepted by the University of Alaska Animal Care and Use Committee.

Statistical Analyses

Body weight data were analyzed using a General Linear Model (GLM) with year of weighing, current reproductive status (lactating, not lactating), and reproductive status as a yearling as factors, and age and age squared as covariates. Summer body weights of females age 2-8 years were included in the analysis.

Future reproduction was analyzed using loglinear modeling (Agresti, 1990; SPSS, 1997) with current reproductive status, reproductive status as yearlings, and year as factors. Because some years had low numbers of observations, only subsets of years and ages containing at least four animals for every combination of age, current reproductive status, and reproductive status as yearlings were selected for analysis. Data from different age females were analyzed separately due to variation in ages represented in different years (Table 1). Models were fitted using all main effects and two-way interactions between year, reproductive status as adults, and reproductive status as yearlings. In all cases the three-way interaction was not significant (P > 0.1) and not included in the model. The most parsimonious model was selected based on the Bayesian Information Criterion (BIC) and likelihood ratio tests (Agresti, 1990; SPSS, 1997).

Survival rates were estimated using mark recapture models with live recaptures (Cormack, 1964; Jolly, 1965; Seber, 1965; Lebreton *et al.*, 1992). Mark-tecapture allowed us to estimate recapture rates so survival rates could be compared directly. Estimates were generated using program MARK (White & Burnham, 1999). Female reindeer born between 1986 and 1991 were included in the model. Individual animal capture histories (age 1 and older) from 1987-1993 were included in the model. Models using year, age, and additive and multiplicative group effects (reproductive status as yearlings) on survival rates and recapture rates were tested. A logit transformation was used for parameter estimation. The best subset of models was selected using Akaike's Information Criterion (AIC), and likelihood ratio tests were used to select from models having similar AIC values.

Table 1. Reproductive status of female reindeer age 2 to 6 during the years 1988-1992 as a function of reproductive status as yearlings. Percentages are percentage of females with distended udders.

		No udder as yearling			Udder as yearling		
Year	Age	No udder	Udder	%	No udder	Udder	%
1988	2	57	100	63.7	11	31	73.8
1989	2	113	116	50.7	36	35	49.3
1989	3	38	73	65.8	10	27	73.0
1990	2	57	117	67.2	22	44	66.7
1990	3	64	184	74.2	11	68	86.1
1990	4	27	85	75.9	8	22	73.3
1991	2	86	62	41.9	4	8	66.7
1991	3	51	97	65.5	23	38	62.3
1991	4	84	116	58.0	20	41	67.2
1991	5	30	58	65.9	14	12	46.2
1992	2	139	122	46.7	16	10	38.4
1992	3	50	57	53.7	4	2	33.3
1992	4	40	82	67.2	18	28	60.9
1992	5	48	88	64.7	16	34	68.0
1992	6	14	31	68.9	7	13	65.0

Results

Incidence of lactation (distended udders) in yearlings from 1987-1997 ranged from 3.9% in 1993 to 39.0% in 1995 (mean = 16%; Fig. 2). The average weight of female yearlings from 1987 - 1997 in June and July was 57.5 kg (standard error of the mean, s_{mean} = 0.57, n = 213).

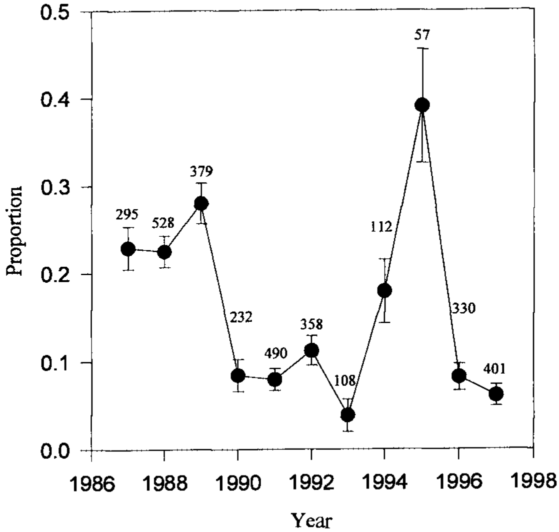

Fig. 2. Proportion of female yearling reindeer on the Seward Peninsula, Alaska, with distended udders (±1 s_{mean}) by year. Numbers above graph are annual sample sizes.

There were significant annual differences in weight (P < 0.0001). Female yearling weights were compared using a two factor GLM (SPSS, 1997), with the factors reproductive status and year, no interaction was tested due to empty cells. Lactating yearling females were heavier (mean = 63.8 kg, s_{mean} = 2.61 n = 14) than non-lactating females (mean = 57.1 kg, s_{mean} = 0.57 n = 199; P = 0.0012), and there were significant annual differences (P < 0.0001).

Although sample size was small, calves weighed during January (~9 months) and subsequently lactating in June, weighed more (mean = 67.8 kg, s_{mean} = 3.74, n = 4) than calves that were not subsequently lactating (mean = 54.9 kg, s_{mean} = 1.36, n = 30; P = 0.0028). The overall mean weight was 56.4 kg (s_{mean} = 1.45).

Subsequent Body Weight

The number of summer body weights collected from females age 2-8 with a known reproductive status as yearlings varied from 9 in 1989 to 136 in 1992. Sparse data made a fully factorial analysis using year and age difficult (Fig. 3) (We were unable to use age nine in the analysis due to small sample sizes in some years. However, years were lumped together in Fig. 3 and so included age 2-9).

The GLM analysis conducted on all summer data from female reindeer age 2 to 8 (Fig. 3) had an R^2 of 43.7% (n = 457) and all independent variables except yearling reproductive status were highly significant (P < 0.0001). The summer weight of currently lactating females (age 2 and older) was lower than the weight of females that were not currently lactating (mean = 76.7 kg, s_{mean} = 0.70, n = 289 vs. mean = 81.5 kg, s_{mean} = 0.81, n = 169). There was no difference in weight due to yearling reproductive status (P = 0.530). The mean weight was 79.5 kg (s_{mean} = 1.00, n = 81) for females that lactated as yearlings and 78.8 kg for females that did not reproduce as yearlings (s_{mean} = 0.57, n = 377).

Subsequent Reproduction

We analyzed the effect on two-year-olds separately. The years 1988-1992 were selected (n = 1186) due to inadequate sample size in other years (Table 1). The model showed a year effect on reproductive status (P < 0.0001) as two year olds but no effect due to previous reproductive status (P = 0.621; Fig. 4). The model fit the data (P = 0.311).

For three-year-olds we included the years 1989-1991 (n = 684). Again, there were annual differences (P = 0.0034) but yearling reproductive status was not significant (P = 0.130). The model fit the data (P = 0.157).

We analyzed data from all females from age 4 to age 6 together and included the years 1990-1992 (n = 936). Results were similar, there were significant annual differences (P = 0.0054) but no differences

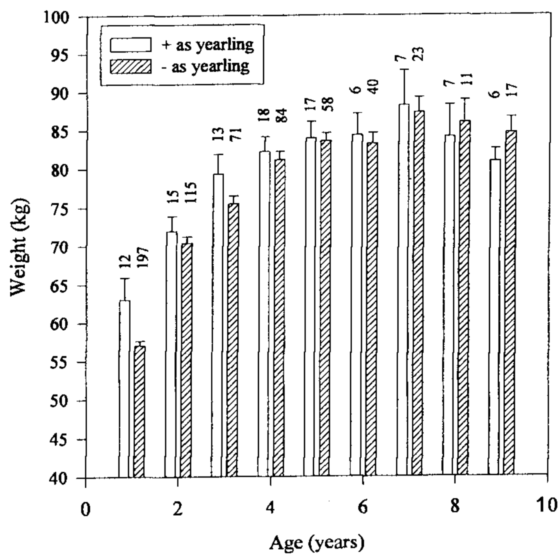

Fig. 3. Weight (±1 s_{mean}) as a function of age for female reindeer on the Seward Peninsula, Alaska. Open bars represent female reindeer with distended udders as yearlings and hatched bars represent females that did not have distended udders as yearlings. Numbers above bars are sample sizes.

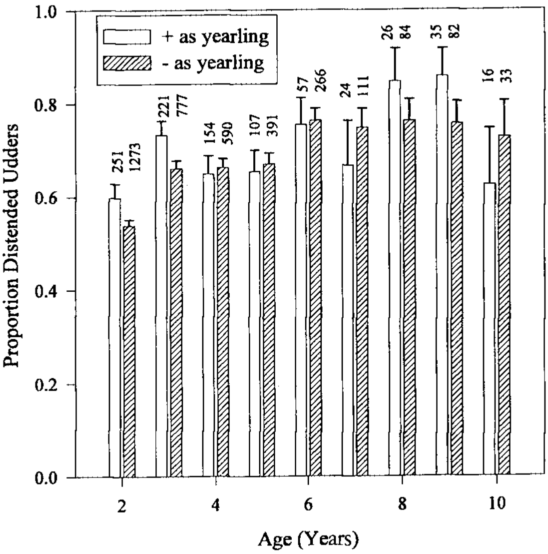

Fig. 4. Proportion of female reindeer on the Seward Peninsula, Alaska, with distended udders (±1 s_{mean}) in June and early July as a function of age. Open bars represent female reindeer with distended udders as yearlings and hatched bars represent females that did not have distended udders as yearlings. Numbers above bars are sample sizes.

due to reproductive status as yearlings (P = 0.789). The model fit the data (P = 0.940).

Subsequent Survival

Mark-recapture models including combinations of age, year, and multiplicative and additive group effects (reproductive status as yearlings) on both survival (ϕ) and recapture rate (p) were run using program MARK. Data entered were recapture histories of females with known reproductive status at one year of age. The years 1987 to 1993 were selected due to small sample sizes in other years.

Based on AIC values the most parsimonious models contained yearly differences in survival and recapture rates but no age effect. The model with the lowest AIC value contained year effects on survival and year and a constant group effect on recapture rate ({ϕ, year ; p, year+group}; Table 2). The likelihood ratio test showed that the reduced model with no group effect on recapture rate {ϕ, year; p, year} was more parsimonious (P = 0.080; Table 2). The Chi-square goodness of fit test showed that this model {ϕ, year; p, year} fit the data (P = 0.54). Estimates of group specific annual survival and recapture rates are shown in Table 3.

Discussion

Daily maintenance energy requirements are twice as high for lactating females as for non-lactating

Table 2. Likelihood ratio tests of mark-recapture models of reindeer survival. The model selected contained annual differences in survival and recapture rates but no difference due to group {ϕ, year ; p, year}. Group represents females that had distended udders as yearlings versus those yearlings that did not have distended udders.

Reduced Model	AIC	General Model	AIC	df	P-value
{ϕ, year ; p, year+group}	6536	{ϕ, year+group ; p, year+group}	6538	1	0.530
{ϕ, year+group ; p, year}	6538	{ϕ, year+group ; p, year+group}		2	0.120
{ϕ, year ; p, year}	6537	{ϕ, year+group ; p, year+group}		3	0.140
{ϕ, year ; p, year}		{ϕ, year ; p, year+group}		2	0.080
{ϕ, year ; p, year}		{ϕ, year+group ; p, year}		1	0.260

Table 3. Survival and recapture probabilities of female reindeer age 1+ years on the Seward Peninsula, Alaska, estimated from the model with year and group specific survival rates and recapture rates {ϕ, year*group; p, year*group}. + indicates females that had distended udders as yearlings, - indicates females that did not have distended udders as yearlings.

	Survival				Recapture			
Year	+	s_{mean}	-	s_{mean}	+	s_{mean}	-	s_{mean}
1987-1988	0.859	0.048	0.917	0.021	0.931	0.038	0.966	0.015
1988-1989	0.926	0.023	0.885	0.015	0.958	0.018	0.933	0.012
1989-1990	0.898	0.022	0.919	0.012	0.920	0.021	0.923	0.012
1990-1991	0.850	0.027	0.836	0.015	0.941	0.020	0.917	0.013
1991-1992	0.811	0.041	0.796	0.024	0.875	0.041	0.800	0.024

females (Chan-McLeod *et al.,* 1994), therefore the high enetgetic costs of lactation were expected to decrease female summer weight gain and survival of yearling females the following winter. However, no negative effects of breeding as calves on future weight gain, reproduction, or survival of female reindeer were observed in this study. Yearling females were apparently able to meet the energetic costs of lactation while increasing in body weight. Lactating yearling females in this study were heavier in June and July and had future reproductive rates, weight gain, and survival rates comparable to non-lactating yearling females.

This study assumes that the presence of a distended udder in June or July is a reasonable indicator of having a calf. Whitten (1995) found that the presence of a distended udder soon after calving correctly predicted parturient cows 91.8 percent of the time, and cows retained their udders 0 to 27 days after a calf died. Because we only included yearlings that successfully raised a calf until June in the distended udders group, yearlings that gave birth but had the calf die early in the summer are included in the non-lactating group. However, the cost of reproduction should be highest in females with calves that survive through weaning.

Increasing energy intake increases protein deposition in lactating females and fat deposition in non-lactating females (Chan-McLeod *et al.,* 1994; Gerhart, 1995). Because the winter diet of lichens is high in energy but low in protein (Person, 1975; Larter & Gates, 1991), lactating females on good winter range may be able to compensate for low fat deposition duting lactation by increasing fat deposition during fall and early winter after lactation (Allaye-Chan, 1991). Chan-McLeod *et al.* (1994) reported that fat deposition was negatively correlated with fat content, therefore lactating females on a high nutritional plane could possibly reach the same body weight as non-lactating females by mid-winter.

Reindeer in general are primiparous at an earlier age than caribou (Dauphiné, 1976; Parker, 1981; Skogland, 1989), but caribou reach a larger adult body size (Skogland, 1989). Therefore although we were unable to find any negative effect of early lactation within this herd, there may be a population level effect of earlier reproduction on reindeer body size (Skogland, 1989). This may have arisen as a response to selective breeding of reindeer or natural selective pressures associated with migratory or predation pressures. Adult female reindeer in this herd have high body weights relative to other reindeer populations (Reimers, 1997). This suggests that relative to other reindeer herds this herd can have both high rates of early primiparity and high adult weights.

Ouellet *et al.* (1997) noted that 42% of caribou calves had enough body fat to reproduce in the fall, but no pregnant calves were observed. Gerhart et al. (1997) suggest that pregnancy rates are influenced by a combination of factors including fat content, skeletal mass, and lactational status. In addition, female caribou of the Porcupine Caribou Herd (PCH) that extended lactation into November were less likely to be pregnant the following year than non-lactating females of the same body weight (Gerhart *et al.,* 1997). Reindeer calve earlier than caribou at the same latitude (White, 1992). Reindeer on the Seward Peninsula calve in late April or early May (Chetkiewicz, 1993). Provided early post-natal nutrition supports lactation, early calving may allow lactating females to wean calves early, reducing the nutritional stress and incidence of lactational infertility described by Gerhart *et al.* (1997).

Reindeer on the Seward Peninsula appear to have a high plane of nutrition and correspondingly high growth rates. The average January weight of female calves in this study was 56.4 kg. This compares favorably to other reindeer and caribou herds (Reimers, 1997). Applying the formula (total body weight = 5.9 + 1.66 * dressed weight) given by Reimers (1997) the average January dressed weight of female calves in this study was 30.4 kg. This weight is higher than August to September calf dressed weights reported by Reimers (25.0 kg; 1983) for a population having a 75% calf pregnancy rate, 25.9 kg for a population having a 47% yearling lactation rate (Reimers, 1972), and the December mean weight of 23.4 kg for a population having a 20% yearling pregnancy rate (Ropstad *et al.,* 1991). Data from bighorn sheep suggest that adverse effects of early primiparity may be higher when nutritional constraints are greater. During a pneumonia epizootic early producers had higher mortality rates than females that reproduced later (Festa-Bianchet *et al*, 1995). Crête *et al.* (1993) reported that George River female caribou exhaust their fat reserves during the first month of lactation while the neighboring Leaf River Herd with better summer range maintains a stable fat reserve.

Females that bred as calves and successfully raised offspring until June were generally heavier in the summer prior to and after calving. It appears these females were more successful than the rest of their cohort in gaining weight during their first summer and maintaining weight during the winter. Therefore, the failure to detect any adverse effects may be masked by higher inherent reproductive potential in animals that bred earlier. If they were able to reproduce without adverse effects on weight gain or skeletal size, they would be expected to be successful as breeders in the future as well. These females may have been genetically superior, offspring of older females, heavier at birth, born earlier, and/or received more milk during lactation. Lifetime reproductive success in bighorn sheep was not influenced by age of primiparity but was positively related to weight at 12 months of age (Festa-Bianchet *et al*, 1995).

We have no estimates of mortality or reproductive success of calves born to yearling females. Young born to early producers are most likely smaller than those born to older females and therefore have higher mortality rates (Skjenneberg & Slagsvold, 1968; Ropstad *et al.*, 1991; Festa-Bianchet *et al*, 1995). Calf survival, and calf body weight in the fall has been shown to be influenced by cow weight in the spring (Lenvik *et al.*, 1988). Therefore calves born to yearlings may be smaller, grow slower, and have lower survival and subsequent reproductive rates than calves born to older females. Ropstad *et al.* (1991) found that 47.4% of calves born to yearlings died. Calf mortality rates may potentially be even higher in Alaskan reindeer due to higher predation rates. High calf mortality rates could decrease the energy expenditure of lactating yearlings, thereby minimizing adverse effects on future performance (White, 1992).

Assuming calf survival is greater than zero, and there are no negative effects on the mothers survival or future reproduction, the result of early reproduction will be a net increase in the expected lifetime reproductive success of the female. In addition, the experience of attempting to raise a calf may increase survival rates of the female's subsequent offspring (Ozoga & Verme, 1986; Reiter & LeBoeuf, 1991). We recorded the presence of udders in June or early July, therefore many of the calves born to yearlings must have survived to midsummer. The ability to recover from the costs of early reproduction likely depends on the quality of forage available during the summer, the time available for foraging, as well as the ability of females to maintain fat reserves during the winter.

Acknowledgements

We thank all the volunteers and employees of the Reindeer Research Program who helped collect these data. N.D. Chelgren and E.A. Rexstad provided statistical advice, M.B. Berger, E.A. Rexstad, R.D. Wadeson, R.G. White, and two reviewers provided helpful comments on the manuscript. We thank L. Davis for the use of his reindeer and support of this project and Kawerak Inc. and the Reindeers Herders Association for their assistance. This is Alaska Agricultural and Forestry Experiment Station paper number J-98-3.

References

Agresti, A. 1990. *Categorical Data Analysis.* John Wiley and Sons. New York, NY.

Allaye-Chan, A. C. 1991. *Physiological and ecological determinants of nutrient partitioning in caribou and reindeer.* Ph.D. thesis, University of Alaska Fairbanks, Fairbanks, Alaska.

Bell, G. 1980. The costs of reproduction and their consequences. – *Am. Nat.* 116: 45–76.

Bergerud, A. T. 1964. A field method to determine annual parturition rates for Newfoundland caribou. – *J. Wildl. Manage.* 28:477–480.

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

Chan-McLeod, A. C. A., White, R. G., & Holleman, D. F. 1994. Effects of protein and energy intake, body condition, and season on nutrient partitioning and milk production in caribou and reindeer. – *Can. J. Zool.* 72: 938–947.

Chetkiewicz, C. B. 1993. *Reindeer* (Rangifer tarandus) *calf productivity and survival on the Seward Peninsula, Alaska.* M.S. Thesis. University of Alaska Fairbanks. Fairbanks, Alaska.

Clutton-Brock, T. H., Guinness, F. E., & Albon, S. D. 1983. The costs of reproduction to red deer hinds. – *J. Anim. Ecol.* 52: 367–383.

Cormack, R. M. 1964. Estimates of survival from the sighting of marked animals. – *Biometrika* 51: 429–438.

Crête, M., Huot, J., Nault, R., & Patenaude, R. 1993. Reproduction, growth and body composition of Rivière George caribou in captivity. – *Arctic* 46: 189–196.

Dauphiné, T. C. Jr. 1976. *Biology of the Kaminuriak population of barren-ground caribou.* Part 4: *Growth, reproduction and energy reserves.* Can. Wildl. Serv. Rep. Ser. No. 38.

Festa-Bianchet, M., Jorgenson, J. T., Lucherini, M., & Wishart, W. D. 1995. Life history consequences of variation in age of primiparity in bighorn ewes. – *Ecology* 76: 871–881.

Gerhart, K. L. 1995. *Nutritional and ecological determinants of growth and reproduction in caribou.* Ph.D. Dissertation. University of Alaska Fairbanks. Fairbanks, Alaska.

Gerhart, K. L., Russell, D. E., Van DeWetering, D., White, R. G., & Cameron, R. D. 1997. Pregnancy of adult caribou: evidence for lactational infertility. – *J. Zool.* (London) 242: 17–30.

Green, W. C. H., & A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. – *Oecologia* 86: 521–527.

Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration- stochastic model. – *Biometrika* 52: 225–247.

Larter, N. C., & Gates, C. C. 1991. Diet and habitat selection of wood bison in relation to seasonal changes in forage quantity and quality. – *Can. J. Zool.* 69: 2677–2685.

Lebreton, J. D., Burnham, K. P., Clobert, J., & Anderson, D. R. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. – *Ecological Monographs* 62: 67–118.

Lenvik, D., & Aune I. 1988. Selection strategy in semi-domesticated teindeer. 4. Early mortality in reindeer calves related to maternal body weight (In Norwegian with an English summary). – *Norsk Landbruksforskning* 2: 71–76.

Lenvik, D., Bø, E., & Fjellheim, A. 1988. Relationship between the weight of reindeer calves in autumn and their mother's age and weight in the previous spring. – *Rangifer* 8: 20–24.

Ouellet, J. P., Heard, D. C., Boutin, S., & Mulders, R. 1997. A comparison of body condition and reproduction of caribou on two predator-free arctic islands. – *Can. J. Zool.* 75: 11–17.

Ozoga, J. J., & Verme, L. J. 1986. Relation of maternal age to fawn-rearing success in white-tailed deer. – *J. Wildl. Manage.* 50: 480-486.

Parker, G. R. 1981. Physical and reproductive characteristics of an expanding woodland caribou population (*Rangifer tarandus caribou*) in Northern Labrador. – *Can. J. Zool.* 59: 1929–1940.

Person, S. J. 1975. *Digestibility of indigenous plants utilized by* Rangifer tarandus. Ph.D. thesis, University of Alaska, Fairbanks, Fairbanks, Alaska.

Reimers, E. 1972. Growth in domestic and wild reindeer in Norway. – *J. Wildl. Manage.* 36: 612–619.

Reimers, E. 1983. Reproduction in wild reindeer in Norway. – *Can. J. Zool.* 61: 211–217.

Reimers, E. 1997. *Rangifer* population ecology: a Scandinavian perspective. – *Rangifer* 17: 105–118.

Reiter, J., & LeBoeuf, B. J. 1991. Life history consequences of variation in age at primiparity in northern elephant seals. – *Behavioral Ecology and Sociobiology* 28: 153–160.

Ropstad, E., Lenvik, D., Bø, E., Fjellheim, M. M., & Romsås, K. 1991. Ovarian function and pregnancy rates in reindeer calves (*Rangifer tarandus*) in Southern Norway. – *Theriogenology* 36: 295–305.

Seber, G. A. F. 1965. A note on the multiple recapture census. – *Biometrika* 52: 249–259.

Skjenneberg, S. & Slagsvold, L. 1968. *Reindriften og dens naturgrunnlag.* (Reindeer husbandry and its ecological principles). Universitersforlaget, Oslo. 332 pp.

Skogland, T. 1989. Natural selection of wild reindeer life history traits by food limiration and predation. – *Oikos* 55: 101–110.

SPSS Inc. 1997. *Systat 7.0: Statistics.* Chicago, Illinois.

Thomas, D. C. 1982. The relationship between fertility and fat reserves of Peary caribou. – *Can. J. Zool.* 60: 597–602.

White, G. C., & Burnham, K. P. 1999. Program Mark: survival estimation from populations of marked animals. – *Bird Study* 46 Supplement: 120–138.

White, R. G. 1992. Nutrition in relation to season, lactation, and growth of north temperate deer. – *In:* Brown, R. D. (ed.). *The Biology of Deer.* Springer-Verlag, New York.

Whitten, K. R. 1995. Antler loss and udder distension in relation to parturition in caribou. – *J. Wildl. Manage.* 59: 273–277.

Manuscript received 12 April, 1999
accepted 1 Novemberr, 1999