Paper presented at The First Arctic Ungulate Conference,
Nuuk, Greenland, 3-8 September, 1991.

Variables influencing survival in four generations of captive-born muskoxen

P. C. Lent and **W. J. Davis**
P.O. Box 101, Glenwood NM 88039, U.S.A.

Abstract: Since 1967, four generations of muskoxen have been born in captivity in Alaska (399 live births, 18 abortions and 47 stillbirths), all derived from 20 females and 8 males captured on Nunivak Island. Analysis of juvenile survival was accomplished by dividing individuals into 7 classes (not born live, born live but not surviving 48 hours, survived 48 hours but < 1 week, survived 1 week but < 1 month, survived 1 month but < 6 months, survived 6 months but < 2 years, survived 2 years). Males were more frequent among live born calves (219:178, $P=.05$), but greater numbers of females survived to 2 years (62:86, $P<.01$). Birthweight ($\bar{X}=9.75$ kg, $N=155$) did not differ between sexes nor did it significantly influence survival. Of 463 individuals, 131 showed some inbreeding but no coefficients of inbreeding exceeded 0.25 and most were less than 0.13. Analysis of variance (Kruskal-Wallis) showed a significant ($P<.05$) difference between survival of inbred and non-inbred individuals. Chi-squared tests showed a greater proportion of non-inbred calves surviving to 2 years ($P<.05$) but no significant differences in perinatal mortality. Offspring of the Nunivak Island cows survived significantly ($P<.01$) longer than those whose mothers were born in captivity, even when only non-inbred calves were compared.

Key words: Muskox, Alaska, breeding success, abortion, inbreeding, mortality

Rangifer, 13 (3): 137—142

Introduction

In 1964 and 1965 a total of 10 male and 23 female muskox *(Ovibos moschatus)* calves was brought from Nunivak Island, Alaska, to the University of Alaska near Fairbanks. Twenty of these females and eight of the males provided the initial breeding stock for a herd that continues today (Wilkinson and Teal, 1984; Bergquist and Murray, 1987). The Nunivak Island stock was in turn derived from 34 animals captured in East Greenland in 1929 (Spencer and Lensink, 1970).

The captive herd of muskoxen in Alaska has been the basis for a domestication effort undertaken to produce qiviut, the fine wooly underhair, in order to support a cottage industry of knitters in rural Alaskan villages. Over the years both the location of the animals being bred for domestication and the organization responsible for the domestication project have changed. Nevertheless, there has been overall continuity of purpose and the project provides a unique opportunity to look at an exceptionally large, long-term data set for a large mammal species bred in captivity. The various personnel responsible for the animals have kept relatively complete and accurate breeding and medical records since 1967, when the first calves were born in captivity.

The study population has occupied three principal sites in Alaska. From 1967 to 1976 the muskoxen were bred near Fairbanks at the University of Alaska. In this subarctic continental climate the animals were maintained on pastures cleared from the taiga many years earlier. Most of the time they had access to wooded areas for browse and shade. Starting in 1975 the stock was transferred to Unalakleet, an area of shrub tundra with a strong maritime influence. The site available for the animals provided insufficient forage and, although some hay and alfalfa pellets were fed, overgrazing had caused significant deterioration of the natural forage base by 1979 (McKendrick, 1981). The Unalakleet operation was closed down in 1984. After a brief stay at a temporary site, the herd was resettled in 1986 on the site of a former farm in the Matanuska Valley near Palmer. Here the animals have about 25 ha of pasture which are supplemented with hay, predominantly a Manchar bromegrass variety, and a pelleted ration (Bergquist and Murray, 1989).

Clearly, achieving a high rate of calf survival is crucial to the success of the muskox domestication enterprise. Several workers have investigated and reported on specific medical conditions causing mortality among infant and juvenile muskoxen. These conditions include contagious ecthyma (Dieterich *et al.*, 1981), *Escherichia coli* infections (Blake *et al.*, 1989), and coccidiosis (Bergquist and Murray, 1987; C. Baker, pers. comm.), each of which has caused significant numbers of calf deaths. However, there has been no overall review of the factors and variables influencing survival of captive-born muskoxen. Because the potential effects of inbreeding were of concern to the herd managers, emphasis was put initially on determining the degree to which inbreeding depression might be influencing juvenile survival.

Materials and methods

The material for our analysis comes from records kept on four generations of muskoxen born in captivity in Alaska from 1967 to 1989. Various degrees of documentation are available for over 400 live births, 47 stillbirths and 18 aborted fetuses. No attempt was made to look at factors causing infertility in these muskox cows, although the numbers of barren cows have been substantial in some years.

Of the births in captivity, 217 occurred in Fairbanks, 128 in Unalakleet, 86 in Palmer and 28 at other locations. Data available for all live births included identity of mother, age of mother, sex of calf, date of birth and date of death. In a few cases for calves surviving more than 6 months the date of death was estimated within a few days.

The identity of the sire was known with certainty in almost all cases. In those few instances where more than one bull had access to the female in question, the father could be determined with a high degree of certainty based on the infant's date of birth. In five cases of uncertainty regarding the male parent, the two males in question were both born on Nunivak Island and therefore the calculation of the coefficient of inbreeding was not affected.

For varying numbers of births other data are available. These include weight of the mother at or around breeding time, based upon one or more live weight data points; weight of the mother around the time of birth, similarly based on one or more actual live weights; weight of calf at birth, and time of birth (Lent, 1991). In almost all cases individual medical records were kept, giving details regarding the cause of death, if known. The information in these individual records has not yet been analyzed in its entirety.

For purposes of our analysis each individual was placed in one of seven survival classes: Not born live, born live but not surviving 48 hours, surviving 48 hours but < 1 week, surviving 1 week but < 1 month, surviving 1 month but < 6 months, surviving 6 months but < 2 years, surviving 2 years.

Using a custom computer program, coefficients of inbreeding were calculated for each possible individual, based upon the additive relationship matrix method (Ballou, 1983). Following the convention used for most studies of inbreeding in which the exact relationship among founder individuals from a wild population is unknown, these individuals were considered unrelated to each other and the calves whose mother and father were both born in the wild on Nunivak Island were assigned coefficients of inbreeding equal to 0. Obviously these founder animals were in some degree related to one another. All were descendants of the 34 animals captured in East Greenland in 1929.

The Nunivak Island population in 1964, at the time of the capture of the initial founder stock, was approximately 450 animals (Spencer and Lensink, 1970). The relatively large size and the demographic history of this population

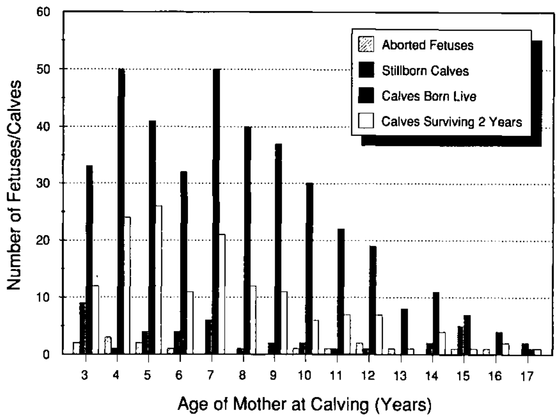

Fig. 1. The outcome of pregnancies by age of mother among captive muskoxen.

(Spencer and Lensink, 1970; Smith, 1984) suggest that no significant inbreeding was occuring in the founder stock.

Results

The reproductive life span of muskox females in captivity extends to 17 years (Fig. 1). There was a propensity for stillbirths and aborted fetuses among cows bred as two-year-olds (13 out of 46 pregnancies or 28 %). Among cows bred at age 14 or older the proportion of the 21 pregnancies not born live increased to 43 %. Among the intermediate age classes (4 through 13) the proportion not born live was only 9.7 %. The effect of the mother's age on the probability of her offspring surviving to 2 years is not clear-cut but possibly this probability declines slightly for mothers over 10 years of age (Fig. 1). However, the three-year-old mothers performed unexpectedly well (36 % of their offspring survived to 2 years vs. 37 % of the population overall).

Males predominated among live born calves (Table 1) and this departure from an equal sex ratio was significant ($\chi^2=4.2$, $P<.05$). Among 47 stillborn calves 16 were male, 23 female and 8 of unknown gender. The predominance of females among stillborn individuals was not statistically significant. The initial survival rates are approximately equal until 1 month of age so that males still comprise 56 % of the calves alive at 1 month. After that point the mortality rate among males is much higher, resulting in a shift in the sex ratio slightly in favor of females by 6 months of age. This trend continues so that by 2 years of age the sex ratio significantly ($P<.01$) favors females. Nearly half (48 %) of females born alive survived to 2 years of age, whereas only 28 % of males did.

Although 131 (28 %) of 468 individuals showed some degree of inbreeding, the coefficients of inbreeding were generally low. Ninety were less than 0.13, 24 ranged from 0.13 to 0.245, and 17 had coefficients of 0.25. A comparison of three classes of calves with varying degrees of inbreeding (Table 2), using a Kruskal-Wallis one-way analysis of variance, showed that the level of inbreeding negatively affected average rank of survival ($P<.05$). Further Chisquared tests indicated significantly ($P<0.05$) higher probabilities of survival to 6 months and to 2 years among live-born non-inbred calves in comparison to live-born inbred individuals. The higher survival rate of non-inbred calves to 1 month of age was not significant.

The probability of survival to 2 years of age was significantly greater for those calves whose mothers were born on Nunivak Island. This was also true when only non-inbred calves were compared (Table 3).

Mean live birth weight for 155 calves was 9.75 kg. This value did not differ significantly (Student's t test, $t=0.15$) between males ($\bar{X}=9.77$ kg, $N=84$) and females ($\bar{X}=9.72$ kg, $N=69$) nor did birthweight significantly influence survival.

Table 1. Survival rates among captive-born muskoxen. Percent surviving of those born live in parentheses.

	Number stillborn	Number born live	Number surviving to: 48 Hours	1 Week	1 Month	6 Months	2 Years
Males	16	219	198 (90%)	180 (82%)	169 (77%)	103 (45%)	62 (28%)
Females	22	180	167 (93%)	145 (81%)	135 (75%)	108 (60%)	87 (48%)
Total	38	399	365 (91%)	325 (81%)	304 (76%)	211 (53%)	149 (37%)

Table 2. Relationship between juvenile survival and degree of inbreeding. Percent surviving of those born live shown in parentheses.

Coefficient of breeding	Number stillborn	Number born live	Number surviving to: 48 Hours	1 Week	1 Month	6 Months	2 Years
0	36	291	268 (92%)	241 (83%)	227 (78%)	161 (55%)	118 (41%)
> 0 < 0.13	6	73	66 (90%)	59 (81%)	52 (71%)	32 (44%)	21 (29%)
0.13–0.25	5	35	31 (89%)	25 (71%)	25 (71%)	18 (51%)	10 (29%)
Total	47	399	365 (91%)	325 (81%)	304 (76%)	211 (53%)	149 (37%)

Table 3. Relationship between place of birth of mother and survival of juveniles. Percent surviving of those born live in parentheses.

	Number stillborn	Number born live	Number surviving to: 48 Hours	1 Week	1 Month	6 Months	2 Years
A. Non-inbred calves							
Nunivak-born mother	13	125	123 (98%)	114 (91%)	112 (90%)	72 (58%)	61 (49%)
Mother born in captivity	22	166	145 (87%)	127 (77%)	115 (69%)	89 (54%)	57 (34%)
B. Inbred calves							
Nunivak-born mother	1	4	4 (100%)	3 (75%)	3 (75%)	2 (50%)	1 (25%)
Mother born in captivity	10	103	92 (89%)	80 (78%)	73 (71%)	48 (47%)	30 (29%)
C. All calves							
Nunivak-born mother	14	129	127 (98%)	117 (91%)	115 (89%)	74 (57%)	62 (48%)
Mother born in captivity	32	269	237 (88%)	207 (77%)	188 (70%)	137 (51%)	87 (32%)

Discussion

We have demonstrated a significantly higher mortality rate to 6 months among inbred muskoxen in comparison to non-inbred juveniles, similar to the findings of Ralls *et al.* (1980) and Ballou and Ralls (1982) for other ungulate species. However, in comparison to the inbred Dorcas gazelles (*Gazella dorcas*), for which they had the largest sample size, the inbred muskoxen showed a lower mortality rate to 6 months (54 % vs. 60 %), and the non-inbred muskoxen had a higher mortality rate than the non-inbred gazelles (45 % vs. 28 %). The first difference presumably reflects the much lower levels of inbreeding in the muskoxen. However, in contrast to the findings for okapi (*Okapia johnstoni*) of De Bois *et al.* (1990), which were limited by a small sample size, we have shown that even low levels of inbreeding (coefficients of inbreeding < 0.13) can have a significant effect on juvenile mortality.

Because of the size of the current herd and the data available regarding the ancestry of living animals, the present herd managers have the ability to eliminate the relatively small additional mortality due to inbreeding. Indeed some of the inbreeding that has occurred early in the history of the project was apparently due to deliberate attempts to inbreed in order to increase qiviut yields (Wilkinson, 1970).

Perinatal mortality among the muskoxen was not affected by degree of inbreeding but was nonetheless high. Benirschke *et al.* (1978) used 10 days postpartum as the cutoff for this period; we used 7 days. Nevertheless, the 30 % perinatal mortality for our muskoxen is considerable greater than the reported 19 % average for bovid species at the San Diego Zoo. Much of this difference can be attributed to the far greater combined proportion of abortions and stillbirths among muskoxen (14 % of all pregnancies vs. only 5.5 % average among bovids at

San Diego Zoo). However, offspring of the Nunivak-born cows experienced only 20 % perinatal mortality and over half of this mortality was due to abortions and stillbirths, proportions similar to those reported by Reindl *et al.* (1993).

The proportion of stillbirths among the muskoxen (10.5 % of total births excluding abortions) is considerably higher than the comparable 4.1 % among 2154 bovid births at the San Diego Zoo reported by Benirschke *et al.* (1978) and 5.5 % among Dorcas gazelles. However, De Bois *et al.* (1990) reported a combined 13.6 % abortions and stillbirths for the okapis. This proportion did not differ significantly between inbred and non-inbred. This finding and the proportion of combined stillbirths and abortions are very similar to our muskox data.

Mild to moderate degrees of placentitis have been described among muskox cows in the captive herd in Saskatoon (Blake and Rowell, 1989) where stillbirths have also been frequent. Age structure of a breeding population can also influence the frequency of stillbirths. In our population the mothers bred as two-year-olds, and those 14 years and older accounted for 33 % of the stillbirths but only 14 % of live births. The greater proportion of females among stillborn calves in our study population, although not statistically significant, also warrants close attention in the future in exploring why stillbirths are apparently so common among captive muskoxen.

The mortality rate to 6 months for non-inbred muskoxen (45 %) is considerably higher than that of the non-inbred representatives of 10 of 12 ungulate species raised at the National Zoological Park (NZP) reported by Ballou and Ralls (1982). Only reindeer and dik-diks had comparably high rates. It is quite probable that the management regime at the NZP is more intensive and access to veterinary care more routine than with the muskoxen. Nevertheless, the higher mortality rates for non-inbred muskoxen lends further credence to the idea that mortality factors other than those tied to inbreeding depression have played an important role in muskox calf survival.

In contrast to both Ralls *et al.* (1980) and De Bois *et al.* (1990) we report significantly better survival among offspring born to mothers who themselves were born in the wild than among offspring born to captive-bred mothers. This difference holds among both inbred and non-inbred offspring. It is possible that the difference was due to location or management regime because most of the births among the Nunivak cows occurred at the original domestication project location in Fairbanks. Either the environment or the original domestication project location in Fairbanks. Either the environment or the management regime at this site might have been particularly favorable. However, the survival to 2 years of offspring born in Fairbanks to non-Nunivak mothers was only 27 % (19 of 71).

When viewing how the juvenile survival rates for the captive population have changed over time, it appears that there have been three peaks in survival rates corresponding with the first years at each of the principal locations that the herd has occupied. These peaks suggest that long-term occupancy has led to either increases in infectious agents or declining nutritional status. Confirming evidence for such a possibility may be found in detailed review of medical records.

Why the probability of survival to 2 years is so much lower for males than for females remains something of a mystery. A few males died as a result of infections received during castrations and others from dehorning efforts, but it does not seem likely that these events were numerous enough to account for the difference. Indeed, the difference is already apparent at 6 months, prior to the age at which these potentially traumatic events oecurred. Perhaps unconsciously or consciously herd managers have given priority in attention and facilities to females. Looking for clues to this difference between the sexes should also be a priority in future examination of the detailed medical and autopsy records.

Acknowledgements

We gratefully acknowledge the assistance of J. McKee and C. Baker of the Musk Ox Development Corporation and S. Robertson of Oomingmak Producer's Cooperative. P. Groves, L. Mealey and J. Truett provided helpful suggestions for improving the paper. We are particularly indebted to Pam Groves for bringing together and summarizing many of the early breeding records. Her diligence made our task much easier. Attendance at the Conference was made possible in part by financial support from BP Exploration (Alaska) Inc.

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Manuscript accepted 15 August, 1993