REPRODUCTIVE PATTERNS OF FEMALE MUSKOXEN IN NORTHEASTERN ALASKA

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ABSTRACT: Reproductive success is an important variable in the dynamics of a re-established population of muskoxen (*Ovibos moschatus*) in the Arctic National Wildlife Refuge, Alaska, USA. From observations of marked female muskoxen between 1982 and 1999, I generated reproductive histories based on the presence or absence of young in late June. I determined age at first reproduction and maximum age at which females successfully reproduced and calculated rates of reproduction by age class and changes in mean reproductive intervals (years between successful reproductive events) over time. Age at first reproduction ranged from 2 to 5 years. Nine of 15 females first reproduced successfully at age 3 years. Thirteen of 17 females >10 years old reproduced successfully at 11-18 years of age; 4 of these had young at age 15-18 years. Two females ceased reproducing at age 6-8 years. Age-related differences in rates of reproduction were not apparent. Reproductive intervals varied within and among individuals. By 1991-1993, most female muskoxen in this population successfully reproduced at intervals of 2-3 years.

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Key words: age at first reproduction, muskox, *Ovibos moschatus*, reproductive history, reproductive interval

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Muskoxen (*Ovibos moschatus*) were re-established near the Arctic National Wildlife Refuge, Alaska, USA, in 1969 and 1970 after an absence of almost 100 years. In regions first occupied, numbers of muskoxen grew rapidly for over a decade (1976-1986), and then decreased and stabilized (1986-1995) (Reynolds 1998), following the classic trend of an introduced ungulate (Caughley 1970). By 1986, mixed-sex groups of muskoxen were dispersing into new regions and production of young declined over time (Reynolds 1998). Rates of production and survival are essential to understanding the dynamics of this re-established population. In ungulates, successful reproduction and survival of juveniles are related to physical condition of females (Cameron et al. 1993, Testa and Adams 1998, Keech et al. 2000). In this study, I wanted to identify critical measures of female reproduction: age at first and last reproduction; reproductive rates at different ages; and mean interval between successful reproductive events. I predicted that young and mature muskoxen had higher rates of reproduction than old females, and that mean reproductive interval (number of years between successful reproductive events) increased over time.

STUDY AREA

The study area is on the eastern Arctic Slope of Alaska, USA, between the Colville River and the Clarence River (Fig. 1). This 24,700-km^2 area encompasses the oil fields at Prudhoe Bay and includes the coastal plain of the Arctic National Wildlife Refuge. The area is underlain by continuous permafrost and is snow-covered for 8-9 months each year. Major landscape features include braided north-flowing rivers

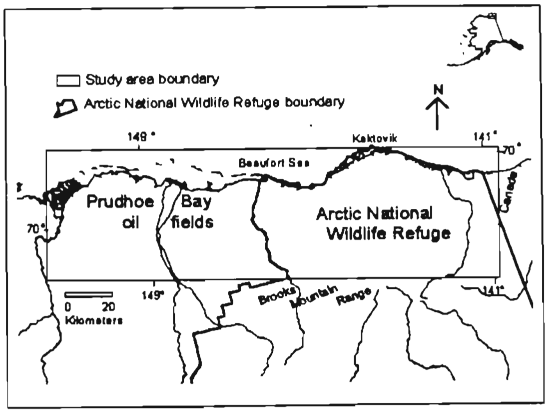

Fig. 1. Muskox study area in northeastern Alaska, USA.

and flood plains, coastal plain and foothills, small areas of thaw-lakes, and rugged mountains on the southern border (Walker et al. 1983). Vegetation is arctic tundra. Shrubs (*Salix* spp., *Dryas integrifolium*) and forbs (*Equisetum variegatum*) grow on partially vegetated gravel bars of rivers. Tussock-shrub (*Eriophorum vaginatum*) and low-shrub (*Salix planifolia, Betula nana*) communities occur on the slopes of rolling hills, and wet-graminoid communities (*Carex aquatilis, Eriophorum angustifolium*) dominate poorly drained flat areas (Bliss 1981). Muskoxen live year-round in the study area where they are preyed on by grizzly bears (*Ursus arctos*) and wolves (*Canis lupus*).

METHODS

From 1982 through 1996, I captured and radiocollared 78 female muskoxen in the study area (Reynolds 1998). I immobilized animals from a helicopter using carfentanil citrate and xylazine (CERVIZINE, Wildlife Pharmaceuticals, Fort Collins, Colorado, USA). Methods used in this study were in accordance with acceptable techniques adopted by the American Society of Mammalogists (Animal Care and Use Committee 1998). Thirty-one females were of known age: 28 were captured as 2, 3, or 4 year olds, when age can be determined from horn characteristics (Oleson and Thing 1989). Three females were marked as yearlings before translocation to northeastern Alaska. I estimated the age of females > 4 years as young adult (5-7 years), mature adult (8-10 years), or old adult (>10 years) based on the size and color of horns and condition and wear of teeth. I recorded the reproductive status of captured females based on examination of teats. Small, undeveloped teats indicated no previous young, elongated teats with no milk indicated young in past years but not in the current year, and teats with milk indicated young in the current year.

Muskoxen in northeastern Alaska are born from late April through mid-June, but reproductive status of marked females could not be determined from aerial surveys. Ground observations, requiring access by helicopter, were conducted annually in late June in conjunction with population composition counts. From 1982 through 1999, I observed marked muskoxen using binoculars or a spotting scope. I defined a successful reproductive event as the presence of young with a radiocollared female in late June. I constructed reproductive histories for 43 marked females that I observed for at least 3 consecutive years. Of these, 26 were observed for 3-5 consecutive years, 15 for 6-9 consecutive years, and 2 for 13-15 consecutive years.

I determined age at first reproduction from 15 known-aged females for which the first reproductive event also was known. I calculated mean age at first reproduction for all years and also compared 2 time periods (1982-1988, $n = 7$ and 1990-1994, $n = 8$) using t-tests (Zar 1984). I determined the oldest ages of successful reproduction by examining the reproductive histories of 17 females estimated to be > 10 years old.

Using 154 cumulative observations of 31 females of known age, I calculated age-specific reproduction as a percentage of females at each age (2-18 years) with young in June. I used linear regression to determine if successful reproduction varied by age (Zar 1984). For this analysis, I used percentages of females successfully reproducing from ages 3 to 10 and combined data for ages > 10 years.

I used reproductive histories from 43 marked females, observed for ≥ 3 consecutive years, to determine levels of reproduction in different individuals. In 3 years, reproductive intervals could range from 0 to 3 years (Table 1). I compared long-term variability in reproductive patterns within and among individuals by examining the reproductive histories of 17 marked female muskoxen that were observed for at least 6 consecutive years. From those animals, I determined ages and dates (year) at the onset of reproduction or nonreproduction in ≥ 3 consecutive years and compared means using *t*-tests (Zar 1984). I calculated mean reproductive intervals for 6 periods that were 3 years in length from 1982-1984 to1997-1999. I used regression analysis (Zar 1984) to test whether changes in mean reproductive intervals occurred over time.

RESULTS

Age at which female muskoxen first reproduced successfully ranged from 2 to 5 years (Fig. 2). One female did not successfully reproduce until 6 years old, but suckled her neonate at age 3 or 4, although that young did not survive until late June. Nine of 15 females (60%) first successfully produced young at age 3 years. The mean age at first reproduction in 1982-1988 was 3.0 years (n = 7), compared with 3.4 years in 1990-1994 (n = 8); that difference was not statistically significant (t_{12} = 2.18, df = 12, P = 0.36).

Thirteen of 17 old females (77%) successfully reproduced after the age of 10. Ten of those females had young within 1 year of death. Four known-aged females were 15-18 years old when they produced

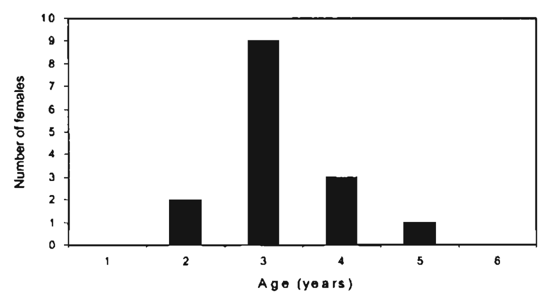

Fig. 2. Age at first reproduction for 15 known-aged female muskoxen observed in northeastern Alaska, USA, 1982-1996.

Table 1. Description of possible reproductive patterns that could occur in 3 consecutive years for muskoxen, Alaska, USA, 1982-1999.

Description of reproduction	Reproductive history[1]	Reproductive interval (number of years between young)
Every year	YYY	0
2 consecutive years	YYN or NYY	1
Every other year	NYN or YNY	1
Once in 3 years	NNY or YNN	2
None in 3 years	NNN	3

[1]Y= with young; N = without young.

young. Two of those females had young the year they died at age 16 and 18; one successfully reproduced for 3 consecutive years before her death. By contrast, 2 females that lived to be 11 and at least 18 years old, did not successfully reproduce after age 6 and age 8 years, although both had young for 3-4 consecutive years before ceasing to reproduce. Two females were alive at the end of the study: one successfully reproduced at age 9, but did not reproduce at age 10 or 11; the other had no young at age12, 13, and 14 years (estimated ages).

Thirty-eight to 60% of females successfully reproduced at 3-8 years of age (Fig 3). Two of 4 females had young at 2 years of age. Females > 10 years old were as reproductively successful as younger-aged animals, but sample sizes were small (Fig. 3). No age-related trends were apparent for ages 3 to > 10 years ($r^2 = 0.049$, $n = 9$, $P = 0.56$).

Levels of reproduction by female muskoxen observed for at least 3 consecutive years could be distinguished (Table 2). Of 43 females, 35% were low, 26% were moderate, 26% were high producers; 14% were mixed producers with both high and low characteristics. Nonetheless, 17 females observed for 6-15 consecutive years showed patterns of reproduction that differed among individuals or changed over time (Table 3). Eight females successfully reproduced for 3-5 consecutive years; however, 3 of these females then ceased to reproduce for 3-11 consecutive years. Five other females also had intervals of 3 or more consecutive years without young. Five females consistently reproduced at 1-2 year intervals for 6-8 years. The presence of young or absence of young for 3 or more consecutive years was not related to animal age ($t_{14} = -0.348$, df = 14, $P = 0.366$) or year when the event began ($t_{13} = -1.494$, df = 13, $P = 0.079$).

Mean reproductive intervals increased significantly ($r^2 = 0.95$, $n = 6$, $P = 0.0009$) over time (Fig. 4). Mean reproductive interval was longest in 1997-1999, but this mean was based on a sample of 3 animals. Not surprisingly, percentages of marked females that reproduced annually for 2-3 consecutive years declined between 1982-1984 and 1991-1993, and percentages of females reproducing at 2-3 year intervals increased (Fig. 5).

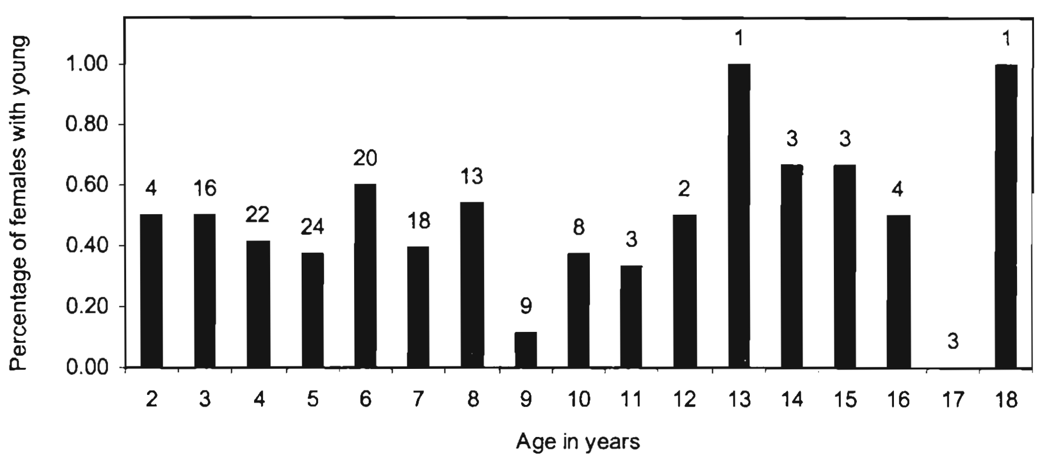

Fig. 3. Age-specific reproduction of marked muskoxen in northeastern Alaska, USA, 1982-1999. Cumulative observations (154) of 31 known-aged females observed in late June were used to calculate percentages of females successfully reproducing at each age. Sample sizes are shown above bars.

Table 2. Levels of production of young in 43 radiocollared female muskoxen observed for at least 3 consecutive years, northeastern Alaska, USA, 1982-1999.

		Number of consecutive years With young		Without young		Young per year of observation	
Productivity level[1]	n	$\bar{x}$	S.E.	$\bar{x}$	S.E.	$\bar{x}$	S.E.
Low	15	_	_	2.7	0.2	0.27	0.03
Moderate	11	1.7	0.1	1.5	0.2	0.57	0.02
High	11	3.5	0.8	0.8	0.2	0.82	0.05
Mixed	6	3.2	0.6	3.9	5.0	0.32	0.06

[1]Low = no young in consecutive years and reproductive intervals of 2- 4 years; Moderate = young every other year or for 2 consecutive years; High = young for 3-5 consecutive years and few reproductive intervals >1 year; Mixed = high and low production.

Table 3. Similarities and differences in long term patterns of reproduction in marked muskoxen observed for 6-15 consecutive years, northeastern Alaska, USA, 1982-1999.

Muskox identification	Age at first observation	Years observed	Reproductive history[1]	Reproductive intervals[2]
008	4	1983-1988	YYYYYN	0001
006	3	1982-1987	NYYYYY	1000
040	8-10	1985-1990	YNYYYN	1101
073	3	1990-1995	YNNYYY	2210
079	3	1990-1997	NNYYYNNY	210122
009	5-7	1982-1996	YYYYNNNNNNNNNNN	0012333333333
053	3	1987-1995	YYYYNNNNN	0012333
087	3	1993-1999	YYNNNNN	12333
068	5-7	1989-1994	NYNNNY	1232
041	5-7	1986-1993	NNNNNYYN	333211
060	4	1989-1994	NNNNYN	3321
081	3	1990-1997	NNNYNYNN	321112
084	3	1992-1997	YNYYNN	1112
049	5-7	1986-1992	NYYNNYY	11221
100	5-7	1994-1999	YNNYNN	1212
021	3	1984-1991	YYNNYNNY	122122
022	5	1985-1997	NYNYNYNYYYNNN	11111110123

[1]Y = year with young; N = year without young.

[2]Interval (years) between young for each set of 3 consecutive years: 0 = 3 young in 3 years; 1 = 2 young in 3 years; 2 = 1 young in 3 years; 3 = no young in 3 years.

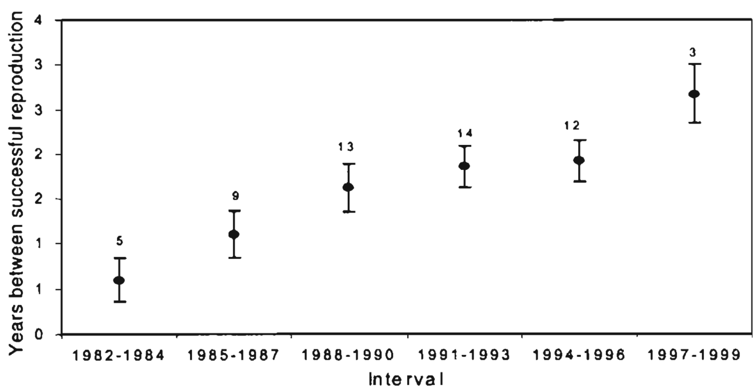

Fig. 4. Changes in mean (± SE) reproductive interval (number of years between successful reproductive events in a 3-year period) of 43 marked female muskoxen, northeastern Alaska, USA, 1982-1999. Sample sizes are shown above error bars.

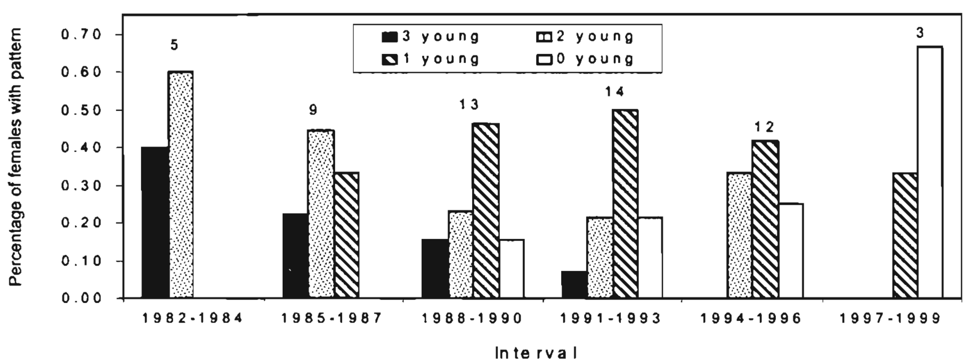

Fig.5. Changes in reproductive patterns of 43 marked female muskoxen observed at 3-year intervals, northeastern Alaska, USA. The legend contains the number of young observed in 3 years: 3 young = annual reproduction; 2 young = young every other year or 2 young in 3 years; 1 young = 1 young in 3 years; 0 young = no successful reproduction in 3 years. Sample sizes are above bars.

DISCUSSION

Most females in this population of muskoxen first reproduced at age 3, but successful reproduction by 2-year-old females also occurred in 1988 and 1991. Jingfors and Klein (1982) observed 2 of 4 2-year-old female muskoxen with young in the study area in late June 1979. Those authors attributed early sexual maturity, annual breeding, and a high rate of reproduction (0.89 young per female of reproductive age) to favorable range conditions in summer. Olesen (1993) estimated that 50% of 2-year-old females produced young in a transplanted population of muskoxen in West Greenland. When habitat conditions are good, sexual maturity in ungulates is reached at an earlier age (McCullough 1979). Successful reproduction by 2-year-old females in this study indicates that habitat conditions were suitable for rapid maturation of some females. High rates of successful reproduction by old-age (> 10 years) animals as well as young females indicates that many females are capable of reproducing from age 3 until near the end of their lives. Reproductive senility was not apparent in this population of muskoxen.

Maternal body condition influences successful reproduction in ungulates (White et al. 1997, Testa and Adams 1998, Keech et al. 2000). Physical condition of females depends on many factors including seasonal availability of forage, energetic costs, current and past reproductive history, and prevalence of parasites and disease. In the study area, parturition and early lactation occur in late April and May when muskoxen are still consuming low-quality sedges and grasses (Wilson 1992). Sedges emerge in early June and abundant dried forage is present until snowfall in September, but abundant green forage is available only from late June until early August. Annual variability in temperature and the length of summer may affect the quality and quantity of forage available in summer and autumn. If the summer is delayed, or winter arrives early, animals may be unable to regain body mass lost the previous winter. Availability of forage in winter depends on snow depth, icing conditions, and the length of the snow season (Wilson 1992). Deep snow also increases energetic costs of foraging and traveling (Klein 1996) and adverse weather may have greater effects on animals at high densities (Messier 1995).

Successful reproduction is influenced by prior reproductive events. After the mid-1980s, most females in this population ceased to reproduce annually (Fig. 5). Successful reproduction at 2-3 year intervals suggests that more than 1 short summer is needed to regain enough body reserves to become pregnant again, maintain a fetus, and nurse young in this population.

Loss of neonates through predation could have influenced the observed shift in successful reproduction. Predation of adult muskoxen by grizzly bears and wolves increased over time (P. Reynolds, unpublished data). In addition to direct mortalities, predators also cause indirect mortalities. When a group runs in panic from a predator, neonates often are left behind and perish (P. Reynolds, unpublished data).

Animal density likely was a factor in changing patterns of reproduction. An increase in the length of reproductive interval was most rapid between 1982-1984 and 1988-1990 when population densities were still increasing (Fig. 5) (Reynolds 1998). Reproductive intervals showed less change between 1988-1990 and 1994-1996 when numbers of muskoxen in the Arctic National Wildlife Refuge were relatively stable (Reynolds 1998). From 1997 to 1999, long reproductive intervals also occurred when young: female ratios in the entire population were low and severe winter weather prevailed (P. Reynolds, unpublished data). Female muskoxen likely reproduce only when there is a high probability of carrying a fetus to term and successfully supporting young through infancy. Variable patterns of reproduction observed in these female muskoxen likely reflect annual variability in weather conditions in the Arctic, increasing predation, and changes in muskox densities that affect forage.

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REFERENCES

ANIMAL CARE AND USE COMMITTEE. 1998. Guidelines for the capture, handling, and care of mammals as approved by the American Society of Mammalogists. Journal of Mammalogy 74:1416-1431.

BLISS, L. C. 1981. North American and Scandinavian tundras and polar deserts. Pages 10-17 *in* L. C. Bliss, O. W. Heal, and J. J. Moore, editors. Tundra ecosystems: a comparative analysis. Cambridge University Press, Cambridge, U.K.

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. Canadian Journal of Zoology 71:480-486.

CAUGHLEY, G. 1970. Eruption of ungulate populations with emphasis on Himalayan thar in New Zealand. Ecology 51:53-72.

JINGFORS, K. T., and D. R. KLEIN. 1982. Productivity in recently established muskox populations in Alaska. Journal of Wildlife Management 46:1092-1096.

KEECH, M. A., R. T. BOWYER, J. M. VER HOEF, R. D. BORTJE. B. W, DALE, and T. R.STEPHENSON. 2000. Life-history consequences of maternal condition in Alaskan moose. Journal of Wildlife Management 64:450-462.

KLEIN, D. R. 1996. Arctic ungulates at the northern edge of terrestrial life. Rangifer 16:51-56.

MCCULLOUGH, D. R. 1979. The George Reserve deer herd: population ecology of a *K*-selected species. University of Michigan Press, Ann Arbor, Michigan, USA.

MESSIER, F. 1995. Trophic interactions in two northern wolf-ungulate systems. Wildlife Research 22:131-146.

OLESEN, C. R. 1993. Rapid population increase in an introduced muskox population, West Greenland. Rangifer 13:27-31.

_______, and H. THING. 1989. Guide to field classification by sex and age of the muskox. Canadian Journal of Zoology 67:1116-1119.

REYNOLDS, P. E. 1998. Dynamics and range expansion of a re-established muskox population. Journal of Wildlife Management 62:734-744.

TESTA, J. W., and G. P. ADAMS. 1998. Body condition and adjustment of reproductive effort in female moose (*Alces alces)*. Journal of Mammalogy 79:1345-1354.

WALKER, D. A., P. J. WEBBER, and K. R. EVERETT. 1983. 1:63,360 scale geobotanical mapping studies in the Arctic National Wildlife Refuge, Alaska. Institute of Arctic and Alpine Research, Plant Ecology Laboratory, University of Colorado, Boulder, Colorado, USA.

WHITE, R.G., J. E. ROWELL, and W. E. HAUER. 1997. The role of nutrition, body condition and lactation on calving success in muskoxen. Journal of Zoology (London) 243: 13-20.

WILSON, K. J. 1992. Spatial scales of muskox resource selection in late winter. M. S. Thesis, University of Alaska, Fairbanks, Alaska, USA.

ZAR, J. H. 1984. Biostatistical analysis. Second Edition. Prentice-Hall, Englewood Cliffs, New Jersey, USA.