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Brief communication

Nursing behaviour as a predictor of alternate-year reproduction in muskoxen

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Introduction

Muskox (*Ovibos moschatus*) females generally produce one calf annually between late-April and early-June. Females nurse their calves until late-January or early-February (White *et al.*, 1989). At the Large Animal Research Station (LARS), 55 calves have been born and survived longer than one month since 1983. On six occasions, females at LARS have continued nursing calves through the following winter, spring, and summer (Table 1). Calves were weaned naturally at approximately 18 months-of-age rather than at the normal 9 months. During this prolonged nursing, the female did not produce another calf. She entered a breeding pause.

Parental investment theory suggests that the offspring's sex may influence the duration of the maternal investment period (Trivers & Willard, 1973). In polygynous species, such as muskoxen,

Table 1. Calves at the Large Animal Research Station, Fairbanks, AK thar have exhibited prolonged nursing from 1983-1994. Calves in italics were used in the analysis. LP = Low plane, HP = High plane.

Cow (Age)	Number of previous calves	Calf	Calf sex	Birth date	Nutritional plane
Red (7)	5	Rufus	male	3 May 1988	LP
Red (9)	6	*Roxanne*	female	26 May 1990	LP
Brown (9)	6	*Anadyr*	female	21 May 1990	HP
Sine (7)	5	Xian	male	15 May 1989	LP
Sine (9)	6	*Sparbo*	male	1 Jun 1991	LP
Unni (11)	7	*Annie*	female	1 May 1994	HP

mothers would be expected to invest more in male offspring as male reproductive success may be increased most dramatically by slight advantages in body condition and body size. Of the six occasions at LARS, there have been the same number of males as females undergoing prolonged nursing (Table 1).

Parental investment theory also suggests that the mother's nutritional condition may influence the duration of maternal investment (Trivers & Willard, 1973). Mothers in poor nutritional condition may invest longer in a calf for that calf to be large enough ro successfully compete with its cohort's members. The female muskoxen at LARS have been divided into high plane and low plane nutritional groups (see Methods) which receive different quality food. Females on the high nutritional plane that are lactating generally weigh more and have more body fat than low plane females (White *et al.*, 1989).

To determine a possible method of predicting when alternare-year reproduction might occur, we performed a retrospective, preliminary, analysis comparing the behavior of females that had and had not undergone breeding pauses. Our hypothesis was that the female's nutritional condition mediates adjustments in reproduction based upon factors other than, but not necessarily exclusive of, their nutritional condition. We suggest that a behavioral feedback between the cow and calf could allow the cow to physiologically monitor, or assess, the nutritional condition of her young through neonare appetite drive, expressed by the calf's nursing behavior. We predict that calves needing prolonged maternal care will nurse longer and more often than normal calves. Also, we predicr that behavioral differences will be most evident during the rut or early post-rut period to balance the female's future reproductive effort with investment in the cutrent offspring. During post-rut, the female may terminate a pregnancy (Rowell *et al.*, submitted) presumable in response to the physiological needs of her calf in an attempt to increase the future reproductive potential of that calf. We used behavior data collected by research volunteers in the LARS Earthwatch program ro test our predictions.

Materials and methods

In 1987, White *et al.* (1989) divided the LARS captive population of muskoxen into high plane (HP) and low plane (LP) nutritional groups, which received different quality food (see White *et al.*, 1989 for description of diets). This variation represents a long or short duration of high-quality food that could occur in the wild. The LP group represenrs a short duration of high-quality food similar to years with early snow in autumn. Both groups receive *ad libitum* hay and grazing. The HP group was given a supplemental ration of commercial high-quality pellets (Quality Texture, Fisher Mills, Seattle, WA; White *et al* , 1989). Beginning in 1988, calves on the HP of nutrition received *ad libitum* pellets and hay at all times via a creep feeder. A creep feeder is a feeder to which only the calves have access. Calves on the LP of nutrition were provided *ad libitum* brome hay.

From 1988, research volunteers from Earthwatch were trained to conduct behavioral observations. Volunteers observed focal animals over a 25-h period using continuous, all-occurrence sampling (Altmann, 1974) on up to three cow-calf pairs within a treatment group from late-May to early-November. Wirhin an observation period, observers recorded all behaviors and behavior changes on a field computer. The computer's internal clock recorded rhe time of each behavior change, which allowed us to calculate the duration of each behavior and between-behavior intervals (Parker *et al.*, 1990; Tiplady, 1990).

Behaviors of cow-calf pairs, as well as individual cows that had previously been observed as a member of a cow-calf pair, were classified into 12 behavior categories: lying, standing, walking, grazing, feeding (from a hay-pellet feeder), drinking, playing, running, creep feeding (from a creep feeder), nursing (and termination of a nursing event), attempting to nurse, and out of sight. Nursing bouts of <5s are classified as unsuccessful nursing attempts (Tiplady, 1990).

We compared nursing behavior for calves that engaged in prolonged nursing with the same behaviors for calves that were weaned at the normal 9 months-of-age. Each calf exhibiting prolonged nursing was paired with a calf weaned at the normal time from the same cow to compare the behavior of a female before she does and does not undergo a breeding pause; these are termed prolonged-normal pairs. All prolonged-normal calf pairs were on the same nutritional plane. To partially standardize for age, development, variations in food supply, and the presence or absence of a bull, we divided the season into fout categories. In the milk-dependent or prerumen function period, calves were <6 weeks of age. Pre-rut calves were 6 - 14 weeks of age, and in the rutting period (from late-Aug. to mid-Oct.) calves

were 12 - 23 weeks of age. During the post-rut period in late-Oct. until early-Nov. calves were 21 - 31 weeks of age. We used the average duration of nursing bouts per day, inter-bout interval, and the total time per day spent nursing as measures of nursing behavior. We then performed a distribution-free randomization test (Potvin & Roff, 1993; p. 1622-1623) on each of the three measures of nursing behavior during each age category for each calf pair and for the groups of normal calves and calves exhibiting prolonged nursing.

Results

We used behavioral data from three prolonged-normal pairs of calves from the same cow, and from a fourth pair of calves born to closely related cows, in the analysis (Table 1). There is a trend for calves in the LP of nutrition group (n = 4) to undergo prolonged nursing more often than calves (n = 2) in the HP of nutrition group (Table 1). Most comparisons between pairs of calves showed no significant differences in any nursing behavior during any seasonal category (Table 2). For pairs in which significant behavior differences were observed, both calves in the pair were the same sex. One pair of calves showed significant differences in one or more behaviors during each of the four categories, however, this pair of calves were born to different cows. Additionally, this pair showed significant differences in all behaviors during the post-rut period. A second pair (Table 2: Scooter-Anadyr) were significantly different in inter-bout interval during the post-rut period as well. Two pairs of calves were significantly different in total time spent nursing per day during rut (Table 2: Scooter-Anadyr and Horton-Sparbo). Two pairs of calves also were significantly different in inter-bout interval during the pre-rumen function period (Table 2: Andree-Roxanne and Horron-Sparbo).

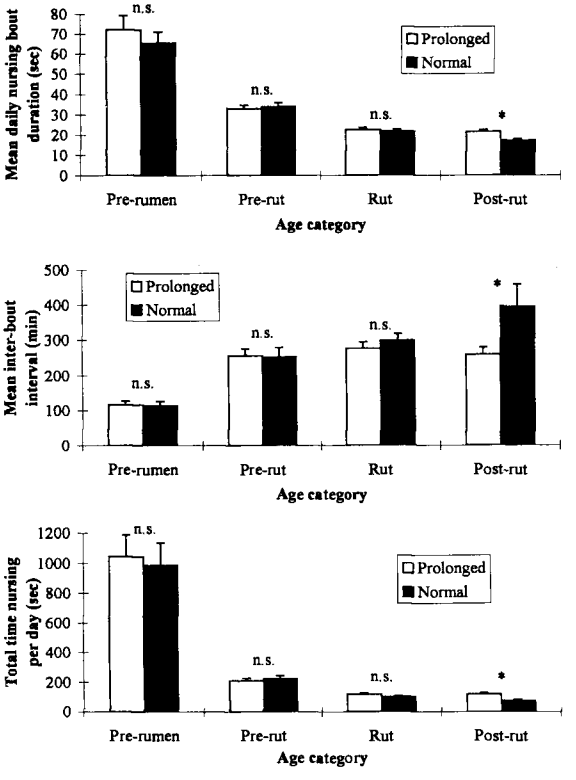

Fig. 1. Comparisons of mean nursing bout duration per day, mean inter-bout interval, and total time spent nursing per day between populations of normal calves and calves with prolonged nursing (n = 4). * = significance $p<0.05$ using distribution-free randomization test. Error bars represent one standard error above the mean. For a definition of the independent variable, see text.

Table 2. Summary of statistical tests using distribution-free randomization (number of randomizations = 10000). Behaviors listed are those for which there were significant ($P<0.05$) differences between calves undergoing normal weaning and rhose with prolonged nursing. Calves in italics were from different cows.

Normal calf	Calf with prolonged nursing	Pre-rumen funcrion	Pre-rut	Rut	Post-rut
Scooter	Anadyr	n.s.	n.s.	Total time per day	Inter-bout interval
Ole	Annie	n.s.	n.s.	n.s.	n.s.
Andree	Roxanne	Inrer-bout interval	n.s.	not available	
Horton	*Sparbo*	Inter-bout interval	Bout duration	Total time per day	All 3 behaviors
Group	Group	n.s.	n.s.	n.s.	All 3 behaviors

Comparisons between the population of normal calves and the population of calves exhibiting prolonged nursing showed similar trends as the pairwise comparisons. There were no significant differences in any behavior during the pre-rumen function, pre-rut, or rut periods (Table 2). However, during the post-rut period, significant differences were found for average duration of nursing bouts, inter-bout interval, and total time spent nursing per day (Figure 1).

Discussion

Our finding significant differences in nursing behavior during the post-rut period supports the hypothesis that female muskoxen use factors other than their nutritional condition to determine their reproductive strategy. After the rut, late-weaning calves nursed longer each day than the normal calves. This is consistent with our prediction that calves needing increased nutrition from the cows may behaviorally signal the cow during the latest time that she may be physiologically responsive to behavioral feedback. We argue that delaying the physiological decision until early in the post-breeding season could be one strategy for minimizing the reduction in a female's lifetime reproductive success associated with producing another calf while still investing in her current calf. The reproductive cost incurred by an error, i.e., weaning of a calf still in need of maternal nutrition, would be a delay in age to first reproduction of the current offspring, and/or poor development of the fetus.

We are unsure of the mechanism by which the female detects that the calf is undernourished. Presumably, calves that are physiologically in need of more nutritional support from the cow return to the cow more frequently in an attempt to nurse. This physiological need could be detected as shorter intervals between nursing bouts (see Loudon & Kay, 1984). Our results support this prediction because the population of calves with prolonged nursing, as well as two individual calves with prolonged nursing, had shorter inter-bout intervals than the normal calves. The calves are successful at getting milk because lactation continued past January. This suggesrs that the cow has the physiological capability to continue investing in such calves. However, the question as to why all calves cannot make use of this capacity still requires further investigation. This is highly relevant as calves of cows on the HP of nutrition also may be nursed through a second summer (Table 1). Since there have been HP calves undergoing prolonged nursing, the phenomenon appears to be based on individual attributes of the cow and calf. We cannot eliminate the hypothesis that factors other than the mother's nutritional condition influence the occurrence prolonged nursing. Thus, neither calf sex nor the plane of nutrition of the mother appears to be an unequivocal predictor of alternate-year reproduction.

We cannot reject the hypothesis that the calf provides a feedback to the dam that may influence her future reproductive effort. Further examination of the body condition of females rhat enter breeding pauses, as well as comparisons of the nutritional condition of calves that do and do not receive prolonged milk intake (i.e., maternal care), may clarify physiological benefits and costs of prolonged lactation. A combination of these physical and behavioral measures may serve as a better predictor of when a female will calve in alternate years.

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