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Relationship between Conception Date and Latitude in Muskoxen

Peter F. Flood & Susan C. Tedesco

Department of Veterinary Anatomy, W.C.V.M., University of Saskatchewan, 52 Campus Drive, Saskaroon, Saskatchewan, Canada S7N 5B4. e-mail: peter.flood@usask.ca

Abstract: It has been suggested that muskoxen calve earlier with increasing latitude but the available data do not seem to have been thoroughly analyzed. Therefore, estimated conception dates (n=657) from a wide range of latitudes were compared. The results indicate that conceptions occur about a month earlier in the arctic than at temperate latitudes. This conclusion is consistent with reported observations of mating behaviour and calving season.

Key words: *Ovibos,* season, calving, reproduction.

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Introduction

In many small mammals breeding begins later with increasing latitude and its timing is closely related to plant phenology and hence food supply (Sadlier, 1969; Bronson, 1985). In larger species with long reproductive cycles such as red deer (Fletcher, 1974), deer of the genus *Odocoileus* (Bronson, 1985; Lee, 1970) and North American wild sheep (Bunnell, 1982; Thompson *et al.,* 1982) there seems to be little or no change in breeding season with latitude provided the profound ecological changes associated with tropical or subtropical environments are excluded. However, none of the analyses of deer or sheep include data from north of the arctic circle. Reindeer, which do extend into the high arctic, breed later the further north they are found (Leader-Williams, 1988). The reindeer data however, include both wild and domestic animals as well as the genetically distinct Svalbard reindeer. Information on domestic sheep is often complicated by genetic differences between breeds but where the Merino was compared at four locations from near the equator to 41°S, there was no clear change in the time of peak incidence of oestrus; nonetheless, there was a very marked concentration of reproductive activity with increasing latitude. Thus the breeding season began sooner and ended later near to the equator (Hafez, 1952).

Seasonally breeding species differ in their characteristic time of birth and muskoxen, for example, calve about 4 - 8 weeks before sympatric caribou (Latour, 1987; Leader-Williams, 1988). Breeds of domestic sheep also differ markedly in the time of their breeding season even when they are kept at the same latitude, and crosses between breeds show intermediate characteristics (Lincoln *et al.,* 1990). Today, wild muskoxen are found from 58–83°N and during the Wisconsinan glaciation (about 20 000 BP) they were numerous as far south as 40°N (McDonald & Davis, 1989). Although there are now no natural muskox populations as far south as this, there are several confined herds that provide a basis for comparison. In a general review of the early literature on muskox reproduction it was suggested that conception occurred earlier at higher latitudes (Teal, 1959) and this was born out by more recent studies (Rowell & Flood, 1988). Because, superficially, advancing reproduction when spring is delayed would seem to be countetintuitive, a more detailed survey of available data was conducted.

Methods

Muskox conception dates were estimated by one ofi two methods. In all cases other than Banks and Victoria Islands a gestation period of 235 days (Rowell *et al.,* 1993) was deducted from the known calving date. For Banks and Victoria Islands the stage of gestation was calculated from the dimensions of fetuses obtained from muskox cows shot on known dates. Regressions published previously (Pharr *et al ,* 1994) were used in the latter estimations. The dates of calving, apart from those from our own records of the Saskatoon herd, were obtained from Holst (1990), Karsten (1986) and Oeming (1965), or were kindly supplied by Gerald Binczik (Minnesota Zoo), Joel and Nancy Bender (Hamilton, Montana), and Peter Lent (Unalakleet, Fairbanks and Palmer). The sources of the fetal dimensions for Banks and Victoria Islands have been outlined previously (*Pharr et al.,* 1994).

Locations for study were selected because the number of known calvings exceeded six with the exception of San Francisco (6 records) and San Diego (5 records) which were included because of their extreme southerly location. Two kinds of record were excluded from the analysis to preclude bias caused by abnormally short pregnancies or differences in fertility between sites. First, isolated calvings (n=5) that occurred more than ten days in advance of the main group of calvings at a given location were removed. Second, all values (n=260) that lay more than 20 days after the first calving in the main group at each location were excluded in order to avoid animals that had not conceived at the first mating. Twenty days is the length of the oestrous cycle in muskoxen (Rowell & Flood, 1988). The total number of records was 657 and 392 of these were included in the final analysis.

The locations for which data are available fell into three groups by latitude; they were the two arctic islands, 5 sites in Alaska and Sweden between 60°N and 65°N, and 11 temperate locations south of 60°N. These are referred to as "Island", "Boreal" and "Temperate" tespectively. The estimated times of conception in these broad groupings were compared using Kruskal-Wallis and Mann-Whitney tests ("Statview" for Macintosh, Abacus Concepts, Inc, Berkeley, California, USA).

Mating may have been artificially delayed in the confined herds at Unalakleet, Fairbanks and Palmer by keeping the males and females separate until a predetermined date early in the breeding season. Fortunately the date when mating was first permitted was known in many cases and varied somewhat from year to year. In order to determine the effect such controlled breeding on the time of conception, the day mating was first permitted was plotted against the estimated day of conception and the results evaluated by simple regression.

Results

Fig. 1 illustrates a strong inverse relationship between estimated conception date and latitude, and includes details of the locations studied. Conceptions occurred over a month earlier on the arctic islands (median date, 19 August) than they did at temperate locations (median date, 29 September). Locations in Alaska and Sweden were intermediate (median date, 20 September). The

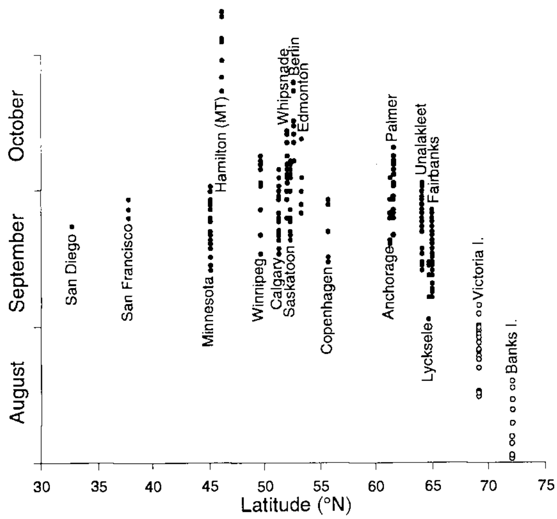

Fig. 1. Estimated muskox conception dates from calving date (solid circles) and fetal dimensions (open circles) plotted against latitude. The location is shown adjacent to each column of points. The total number of observations at each location and the number shown on the graph after truncation (in parentheses) are: Anchorage, 6 (6); Banks Island, 39 (19); Berlin, 18 (12); Calgary, 39 (22); Copenhagen, 22 (5); Edmonton, 7 (7); Fairbanks, 207 (152); Hamilton, Montana, 8 (7); Lycksele, 12 (6); Minnesota, 43 (27); Palmer, 32 (18); San Diego, 5 (1); San Francisco, 66 (3); Saskatoon, 30 (16); Unalakleet, 85 (44); Victoria Island, 31 (18); Whipsnade, 28 (18); Winnipeg, 21 (12).

differences between the Island, Boreal and Temperate groups were all significant ($P<0.0001$). The distribution of the points could either be seen as a smooth curve or a "broken stick" with the point of inflection close to 60°N.

As expected, in those confined herds in which the bulls were only allowed access to the females in the breeding season, the later the bulls and cows were put together the later conceptions occurred. In addition, the later in the year that mating was first permitted, the shorter was the interval to conception. It therefore appears that when the bull was introduced relatively early in the year, many cows had not begun to show oestrus. Thus the controlled mating system used in Palmer, Fairbanks and Unalakleet probably had little effect on the conception dates that were included in the analysis owing to the use of the truncation procedure. Further evidence for this view comes from the dates of unconstrained conceptions at Anchorage and Lycksele (Fig. 1) and the fact that none of the estimated dates of conception were less than eight days after the bulls were introduced when introduction occurred early in the season.

Discussion

Our results support Teal's (1959) contention that calving in muskoxen occurs earlier at higher latitudes. The data in Fig. 1 are significant but they depend in part on the assumption that the two methods used to estimate the time of conception yielded comparable dates. While it is most unlikely that the two methods gave identical results, we would argue that they are sufficiently close to allow the inferences made. The most obvious support for this view comes from inspection of the points in Fig. 1; they can be seen to form a continuous band with no obvious break where the method of analysis changed. Further, the data show the same trends in the parts of the curve based on fetal dimensions alone and on birth dates alone.

If the gestation period used in the analysis were too short, the advance in breeding season with latitude would be ovetestimated. The value we used (235 days) was based on detailed observation of ten pregnancies in young muskoxen kept in Saskatoon and may not be typical of older animals or animals in the atctic. The period of 8 months given by Groves (1992), which has presumably served as a useful rule of thumb, is seven days longer (adding the relevant months which always include February). If this gestation period had been used in our estimations, it would only marginally change the conclusions.

The artificial constraints placed on the beginning of the breeding season in Fairbanks, Palmer and Unalakleet are likely to have reduced the difference between the Alaskan and Temperate conception dates, while exaggerating the difference from the Island dates. Overall, without this effect the curve formed by the points in Fig. 1 would have been smoother. Even so we suspect that the induced error was small for the reasons given at the end of the results section. However, as in sheep and goats, the onset of oestrus may have been artificially delayed by the absence of males at the beginning of the breeding season (Lindsay, 1991).

There is substantial though incomplete agreement between the present analysis and behavioural reports in the literature (Fig. 2). The observed mating period on Bathurst Island (Gray, 1987) and the period of births at Kangerlussuaq (Olesen, 1993) match the present results particularly well. Limited observations on Ellesmere Island (Tener,

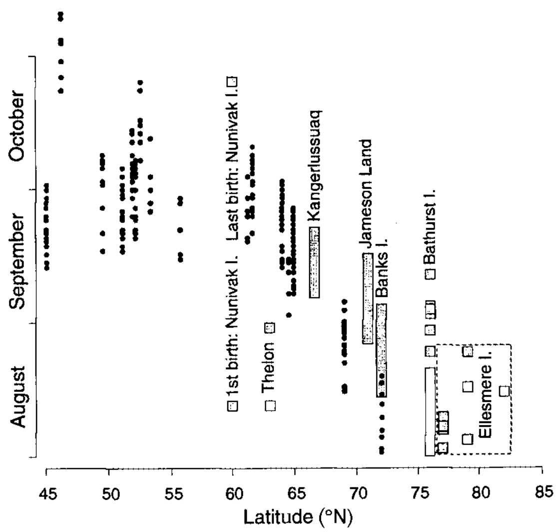

Fig. 2. Estimared muskox conception dates (solid circles) compared with observations of mating behaviour in the wild (open rectangles) and conception dates corresponding to individual calvings or calving periods reported in the wild (stippled rectangles). All ate shown plotted against latitude (°N). The locations for the data shown by the rectangles are indicated. The dotted recrangle encloses observations on Ellesmere Island. The remaining locations are shown in Fig. 1. The behavioural information was obtained from Tener, 1965; Rowell, 1980; Thing, 1984; Gray, 1987; Latour, 1987; Lent, 1988 and Olesen, 1993.

1965; Rowell, 1980) also broadly conform to the expected trend. However, births on Bathurst Island (Gray, 1987) were later than would have been expected from mating behaviour, perhaps because conception was delayed by nutritional stress, and the estimated time of the earliest births on Banks Island (Latour, 1987) was two weeks later than predicted by measurement of fetuses. The reported calving season on Jameson Land on the East coast of Greenland (Thing, 1984) was also later than expected. The information for Nunivak Island (Lent, 1988) and the Thelon Game Sanctuary (Tener, 1965) has been included for completeness but it is so fragmentary that it adds little. To conclude, the information on calving season summarized in Fig. 2 supports the view that calving occurs earlier at higher latitudes even though the overall timing is somewhat later than would have been expected from fetal measurements.

The reason for the delay in reproduction seen at more southerly locations is not clear. The effects of captivity alone do not seem to provide an adequate explanation because the Boreal animals calved before the tempotate ones though both were confined. Nonetheless, the brief superabundance of high quality forage available during the arctic summer is hard to duplicate in captivity and we are loath to reject the possibility that it advanced the breeding season.

Two hypotheses involving photoperiod receive little support from the present data. The first and simplest is that reproduction in muskoxen occurs at a fixed period of about 100 days after a critical daylength is reached around the vernal equinox. If the critical daylength were greater than 12 hours of light it would occur earlier at higher latitudes. The data as a whole do not fit this concept; the changes in breeding season north of 60°N are too great to be explained by any daylength that occurs further south. If only latitudes north of 60°N are considered, the time of conception can be neatly described by saying that it occurs about 108 days after the first day when the sun is in the sky for more than 19 h. Because the daylength and the lag period were chosen to fit the data, this observation implies little about causation but it does provide a simple means of estimating the time of the breeding season.

The second hypothesis depends on the assumption that the circadian day is shorter than the 24 h day. Thus in the high arctic, during the continuous light of summer, muskoxen might switch to the shorter circadian day in the absence of other cues and arrive at the breeding season sooner. This explanation fails to account for the change in breeding season with latitude seen south of the Arctic Circle and conflicts with the observation that the muskox circadian day differs little, if at all, from the 24 h day (Tedesco, 1996). A phenomenon which may or may not be related is seen in rams in which melatonin secretion has been abolished by pinealectomy or cranial cervical ganglionectomy. Such animals come into breeding condition several weeks earlier than their intact controls (Lincoln *et al.,* 1989). It is possible that the suspension of melatonin secretion caused by the continuous light of the arctic summer has a similar effect. Again, an explanation based on this phenomenon fails to explain the change in breeding season occurring south of the Arctic Circle.

Another factor that may influence the onset of the breeding season is the rate of change in daylength: for example in Saskatoon, daylength increases by seven minutes a day at its maximum in March, but at 71°N the increase can be over 27 minutes. In ewes, a change in daylength, rather than exposure to days of a specific length, is necessary to entrain the circannual reproductive cycle (Robinson & Karsch, 1987), and the amount of change in daylength affects the magnitude of the response (Robinson *et al.,* 1985). Therefore, the dramatic changes in photoperiod occurring in the arctic immediately after the period of continuous winter darkness may provide a more potent stimulus than the more moderate events further south.

Finally, in sheep, high temperatures delay the onset of reproduction (Dutt & Bush, 1955), increase embryonic loss (Bell, 1987) and adversely affect placental development (Bell *et al.,* 1989): high ambient temperatures may have similar effects on muskoxen kept at temperate latitudes. In muskoxen, delaying reproduction somewhat at times of nutritional stress has a possible medium-term advantage in that it would shorten the energetically demanding period of lactation that normally occurs prior to the availability of new growth. It is harder to see how reproductive delay would be an appropriate response to thermal stress but perhaps stress is a poorly differentiated event. It would be interesting to see if nutritional stress at arctic latitudes delays the calving season.

In conclusion, it seems that breeding season in muskoxen changes little through the temperate latitudes as in other ruminants, but is advanced from about 60°N northwards. The opposite is apparently true of reindeer. Perhaps in muskoxen, the calf's maturity on entering the arctic winter is more critical than its mother's need for good quality nutrition during early lactation. This would be consistent with the substantial fat reserves often found in pregnant muskoxen in late winter (Adamczewski *et al.,* 1996). We see no single convincing explanation of the change in breeding season with latitude though there are a variety of mechanisms that may play a part. Perhaps the phenomenon has many causes.

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