

# Synchrony between caribou calving and plant phenology in depredated and non-depredated populations

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**Abstract:** Two main hypotheses have been proposed to explain reproductive synchrony exhibited by many species of large herbivores: the predation hypothesis and the seasonality hypothesis. Although examples supporting both hypotheses have been presented, no study has compared the intraseasonal progression of parturition and plant phenology in depredated and non-depredated populations of large herbivores. We monitored, on a daily or near-daily basis, the progression of the caribou (*Rangifer tarandus*) calving seasons in two populations: the Caribou River population in Alaska, U.S.A., where predators of caribou are present and the Kangerlussuaq-Sisimiut population in West Greenland where such predators have been absent for approximately 4000 years. Simultaneously, we quantified directly the phenological progression of caribou forage plants on spatially replicated plots in both study sites. Parturition was significantly more synchronous in the West Greenland (predator-free) population than in the Alaskan (depredated) population. Progression of the calving seasons in both populations was highly synchronized to the progression of forage plant phenology, and the slopes of these relationships were statistically indistinguishable, with 50% of births having occurred when approximately 60%–70% of forage plant species were emergent. These results document clear synchronization of the timing of parturition by caribou to plant phenology, regardless of predation pressure.

**Résumé :** Deux hypothèses principales, celle de la prédation et celle de la saisonnalité, ont été mises de l'avant pour expliquer le synchronisme de la reproduction chez plusieurs espèces de grands herbivores. Bien qu'il existe des exemples à l'appui de chacune des hypothèses, aucune étude ne compare la progression de la parturition au cours de la saison et la phénologie des plantes chez des populations de grands herbivores, soumis ou non à la prédation. Nous avons suivi, sur une base journalière ou presque, la progression des saisons de vêlage chez deux populations de caribous (*Rangifer tarandus*), la population de la rivière Caribou en Alaska, États-Unis, où il existe des prédateurs, et la population de Kangerlussuaq-Sisimiut au Groenland occidental où il n'y a pas de prédateurs depuis environ 4000 ans. En même temps, nous avons quantifié directement l'évolution phénologique des plantes de fourrage du caribou sur des parcelles dédoublées dans l'espace aux deux sites. La mise bas est significativement plus synchronisée chez la population du Groenland occidental (en l'absence de prédateurs) que chez celle d'Alaska (avec prédateurs). La progression de la saison de vêlage chez les deux populations est fortement synchronisée avec l'évolution de la phénologie des plantes de fourrage : les pentes des deux relations ne peuvent se distinguer statistiquement et 50 % des naissances ont eu lieu lorsque environ 60 % – 70 % des espèces de plantes de fourrage ont poussé. Ces données montrent une synchronisation claire du moment de la mise bas chez le caribou avec la phénologie des plantes, indépendamment de la pression de prédation.

[Traduit par la Rédaction]

## Introduction

Early studies of reproductive synchrony in colonially nesting birds led to the hypothesis that such behavior had evolved through reduced risk of predation to individual offspring (Darling 1938). This “predator swamping” hypothesis was subsequently forwarded to explain the highly synchronous season of births in wildebeest (*Connochaetes taurinus*)

in the Ngorongoro Crater, Tanzania (Estes 1976). Wildebeest born into large groups at the peak of the highly synchronized calving season were argued to be less likely to suffer predation than those born early or late (Estes 1976; Estes and Estes 1979). In part, advantages of being born during the peak of the birth season derive from the greater numbers of potential prey per predator during the peak, but benefits may also be derived from being born into groups of vigilant mothers congregating during the peak of calving (Rutberg 1987; Bøving and Post 1997).

Great interest in the phenomenon of reproductive synchrony arose from the seminal studies by Estes (1976) and Estes and Estes (1979), with similar patterns of highly synchronous parturition having been documented in many species, including bighorn sheep (*Ovis canadensis*) (Festa-Bianchet 1988), white-tailed deer (*Odocoileus virginianus*) (McGinnis and Downing 1977), Dall's sheep (*Ovis dalli*)

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(Rachlow and Bowyer 1991), roe deer (*Capreolus capreolus*) (Gaillard et al. 1993), mule deer (*Odocoileus hemionus*) (Bowyer 1991), and caribou or wild reindeer (*Rangifer tarandus*) (Skogland 1989; Post and Klein 1999). Rutberg (1987) argued, however, that it is unlikely for synchronous parturition to have evolved from asynchronous parturition solely in response to predation on newborns. Rather, predation on early- and late-born individuals might, according to Rutberg (1987), increase synchrony of parturition in populations in which seasonal birth peaks are timed to coincide with seasonal peaks in resource availability.

The "seasonality hypothesis" predicts that selection acting through intraannual variation in weather and resource availability results in optimization of the timing of parturition by individuals to coincide with the seasonal peak of food availability (Sadleir 1969; Sekulic 1978). According to this hypothesis, synchrony within populations may result from selection on the timing of parturition by individuals and the consequent variation in their own reproductive success and that of their offspring as influenced by seasonal variation in resource availability (Rutberg 1987; Ims 1990). Indeed, the considerable degree of geographic variation within some species in the average timing of parturition among populations suggests that environmental factors, which also vary geographically, influence timing of reproduction. In Norwegian wild reindeer, for example, timing of parturition may vary among populations by as much as 2–3 weeks, presumably because of combined influences of environmental conditions on forage availability and physical condition of reproductive females (Reimers et al. 1983). In further support of the seasonality hypothesis, Skogland (1989) reported that the peak of parturition varied by 34 days among six populations of wild reindeer in Norway, with southern populations calving earlier than northern populations, and that the populations calving later also calved over a shorter period, i.e., more synchronously.

Many recent studies of reproductive synchrony in large mammals that have taken into account seasonal variation in resource availability have urged reevaluation of the predator swamping hypothesis. Evidence from multiannual studies of depredated populations of Dall's sheep (Rachlow and Bowyer 1991) and moose (Bowyer et al. 1998) in Alaska, U.S.A., and of mule deer (Bowyer 1991) in California, U.S.A., indicate that, despite predation on newborns, timing and synchrony of parturition in the focal populations appear to relate to long-term climatic patterns, a predictor of temporal variability in resource availability, and their influence on offspring survival. In northern environments, in particular, the short season of plant growth results in a rapid peak in, and deterioration of, digestibility and nutrient content of plant tissues associated with the progression of plant phenology (Klein 1990). Mammalian herbivores inhabiting such environments are therefore faced with a brief season of peak forage quality in which they must maximize nutrient intake to support the costs of lactation. As a consequence, large herbivores adapted to reproducing in the far north, such as caribou and wild reindeer, display considerable selectivity and sensitivity to patterns of plant phenology in their use of calving sites (Eastland et al. 1989; Fancy and Whitten 1991; Nellemann and Thomsen 1994; Vistnes and Nellemann 2001). Here, we expand upon earlier work (Post and Klein

1999) in which we documented synchronous parturition in two populations of caribou in Alaska that were depredated by brown bears (*Ursus arctos*) and wolves (*Canis lupus*). Progression of the calving seasons in these depredated populations appeared to track closely progression of plant phenology in the two study sites, although relationships between synchrony of calving and plant phenology were not explicitly investigated by Post and Klein (1999). Using similar data on caribou calving and plant phenology in West Greenland, where natural predators of caribou have been absent for approximately 4000 years (Meldgaard 1986), we compare the timing and synchrony of calving, and their relationships to plant phenology, between depredated and non-depredated populations.

## Materials and methods

### Study sites

We observed congregations of calving caribou in the Caribou River (CR) population in Alaska in 1992 and in the Kangerlussuaq-Sisimiut (KS) population in West Greenland in 1993 and 2002; data from 1993 are presented here only for comparison with those from 2002. The CR population inhabits subarctic, mesic, and wet-sedge meadows at the southwestern terminus of the Alaska Peninsula (55°45'N, 161°30'W) (Post and Klein 1999). The area is treeless with a strongly maritime climate, and calving sites are dominated by short-stalk sedge (*Carex nesophila*), marsh cinquefoil (*Potentilla palustris*), and field horsetail (*Equisetum arvense*) (Post and Klein 1996). During the calving season (late May – early July) on the CR calving range, daily minimum and maximum ambient temperatures average 5.8 and 14.6 °C, respectively (Bøving and Post 1997). The KS population occupies low arctic coastal and inland ranges in West Greenland, in the area bounded by the Davis Strait to the west, the Inland Ice to the east, Nordre Isortoq River to the north, and the Sukkertoppen Ice cap to the south (66°–67°N, 50°–52°W) (Bøving and Post 1997). During and following the calving season, the KS population occupies the farthest eastern inland portion of its range, at the western edge of the Inland Ice (Thing 1984; Bøving and Post 1997). This area is characterized by a dry, continental climate with mean daily minimum and maximum temperatures during the calving and postcalving seasons (late May – late June) of 1.6 and 12.5 °C, respectively (Bøving and Post 1997). The KS calving range comprises east–west running ridges with xerophyllic plant species dominating the warm, dry south-facing slopes, including the graminoids *Kobresia myosuroides* and *Carex supina*, interspersed with patches of blue–green willow (*Salix glauca*) and dwarf birch (*Betula nana*) (Thing 1984; Bøving and Post 1997). North-facing slopes on the KS calving range experience greater snow accumulation during winter and later snowmelt and are dominated by dense Labrador tea (*Ledum palustre*) heath, while mesic lowlands are characterized by *Poa pratensis* greens (Thing 1984; Bøving and Post 1997). Whereas on the calving range of the CR population, large predators are common and include wolves, brown bears, lynx (*Lynx canadensis*), golden eagles (*Aquila chrysaetos*), coyotes (*Canis latrans*), and wolverines (*Gulo gulo*) (Post 1995; Post and Klein 1999), large predators of caribou have been absent from West Greenland for approxi-

mately 4000 years and no predation, human or otherwise, occurs on the KS calving range (Meldgaard 1986; Klein et al. 1987).

### Collection of calving data

In both study sites, we observed groups of preparturient and parturient female caribou on a daily or near-daily basis. Observations of females in the CR population began and ended on 30 May and 5 July, respectively, whereas observations of females in the KS population began and ended on 5 June and 19 June, respectively. We focused our efforts on observing congregations of females in areas where they occurred predictably and observed a minimum of 25 adult females on each day. On each day of observation, we recorded the numbers of adult females and calves observed using spotting scopes and binoculars from elevated vantage points. Animals under observation were not aware of our presence. The method that we used does not assume, or require, that the individuals observed each day were the same individuals observed on other days (Caughley 1977).

### Analysis of calving data

Following methods in Caughley and Caughley (1974), Caughley (1977), and Skogland (1989), we converted our data from proportion calves versus date to cumulative percent births versus date. We used probit analysis (Finney 1947) to estimate mean dates of parturition (Caughley and Caughley 1974) and nonlinear regression to estimate the length of each calving season (i.e., its synchrony) as the difference between the dates of 10% and 80% births. Further details of methods of collecting and analyzing parturition data are given in Post and Klein (1999).

### Collection and analysis of plant phenology data

We established 10 (CR) and 20 (KS) 0.5-m<sup>2</sup> phenology plots in each of the study sites and monitored them at regular intervals of 3 days (CR study site) or daily (KS study site). Plots were divided among two (CR) and four (KS) meadows of comparable species composition, aspect, and elevation within each study site; these meadows were chosen so as to be representative of, and adjacent to, the areas where parturient caribou were observed. Phenology plots were placed randomly within each meadow and spaced a minimum of 50 m apart; meadows containing the plots were separated by approximately 1 km within each study site.

On each visit to the phenology plots, we recorded the names and numbers of plant species emergent in each plot. The final numbers of plant species emergent differed between study sites, with the CR site being more speciose ( $18 \pm 1.3$  (mean  $\pm$  SE) species per plot) than the KS site ( $6.8 \pm 0.4$  species per plot) (one-way ANOVA comparing means:  $F_{[1,28]} = 112.4$ ,  $P < 0.001$ ). Within neither the CR nor the KS study site, however, did the final number of species emergent differ among plots between the meadows sampled (CR:  $F_{[1,8]} = 1.3$ ,  $P = 0.29$ ; KS:  $F_{[3,16]} = 2.9$ ,  $P = 0.07$ ). Because of differences in species number between CR and KS, to make our analyses comparable between ranges, we transformed daily numbers of species emergent to daily proportions of the final number of species emergent in each plot on each range. Using the final number of species emergent in each plot at the end of monitoring, we back-calculated the

percentage of this final number in an emergent state on each day of observation prior to the last day of monitoring. To analyze the progression of plant phenology on each study site, we used nonlinear regression to estimate the date of 50% emergence in each study site, the number of days between 10% and 80% emergence (i.e., synchrony), and the rate of forage species emergence in each study site as the slope of the relationship between percent emergent and Julian date (calculated from day 1 = 1 January). Further details on methods of monitoring and analyzing plant phenology data are given in Post and Klein (1999).

### Comparisons of parturition between populations and analysis of parturition in relation to phenology

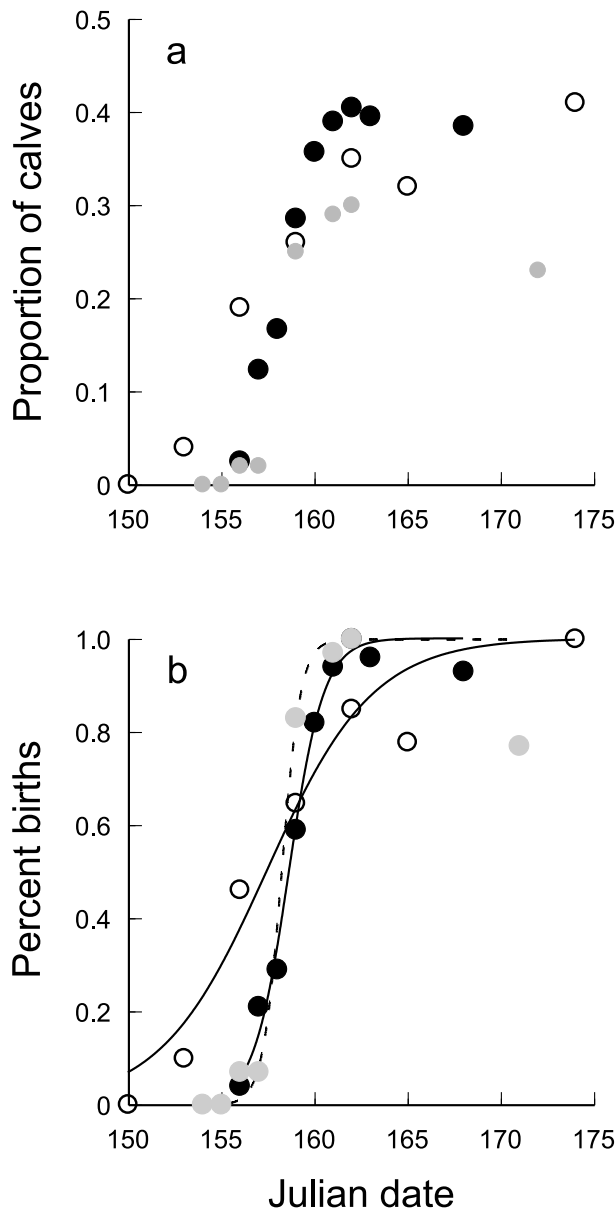
We compared the synchrony of calving between populations using an approximation of the Student's *t* test for regression coefficients (Zar 1984). In this approximation, 95% confidence intervals of regression coefficients, in this case the slopes of the regressions of percent births versus Julian date, are compared against each other and the regression coefficients deemed to be significantly different ( $P < 0.05$ ) if the confidence intervals do not overlap (Bjørnstad et al. 1995). The same analysis was applied to test for differences in the synchrony of plant phenology between study sites and for differences in the relationships between the progression of calving and plant phenology in the two populations. All analyses were performed with SPSS version 10.0 (SPSS Inc. 1999).

## Results

First calves were observed on 31 May (1992) and 5 June (1993 and 2002) in the CR and KS populations, respectively (Fig. 1a). Progression of the 1993 and 2002 calving seasons in the KS population were comparable, although overall calf production was higher in 2002 (Fig. 1a). The mean date of calving in the CR population was 5 June (Post and Klein 1999), and the number of days between 10% and 80% births was estimated at 10 days (nonlinear regression,  $R^2 = 0.95$ ) (Post and Klein 1999). In the KS population, the mean date of calving was 8 June (probit,  $R^2 = 0.90$ ), and the number of days between 10% and 80% births was 5 days (nonlinear regression,  $R^2 = 0.98$ ). Hence, calving started later but was more synchronous by 5 days in the KS population than in the CR population (Fig. 1b).

As with the seasons of calving, emergence of forage plants commenced earlier in the CR study site than in the KS study site: 50% of the final number of species observed were emergent on 24 May in the CR site and on 7 June in the KS site (Fig. 2a). Similarly, plant phenology progressed more rapidly in the KS site, with 8 days passing between 10% and 80% emergence (nonlinear regression,  $R^2 = 0.98$ ) compared with 43 days in the CR site (nonlinear regression,  $R^2 = 0.98$ ) (Post and Klein 1999). Because this analysis may be sensitive to differences in the lengths of observation periods in the two study sites, we repeated these analyses using the subset of CR data that overlapped the KS data. With this subset, 50% of the final number of species observed were emergent in the CR site on 26 May, and the number of days between 10% and 80% emergence was 21; hence, forage plant emergence commenced later and was more synchro-

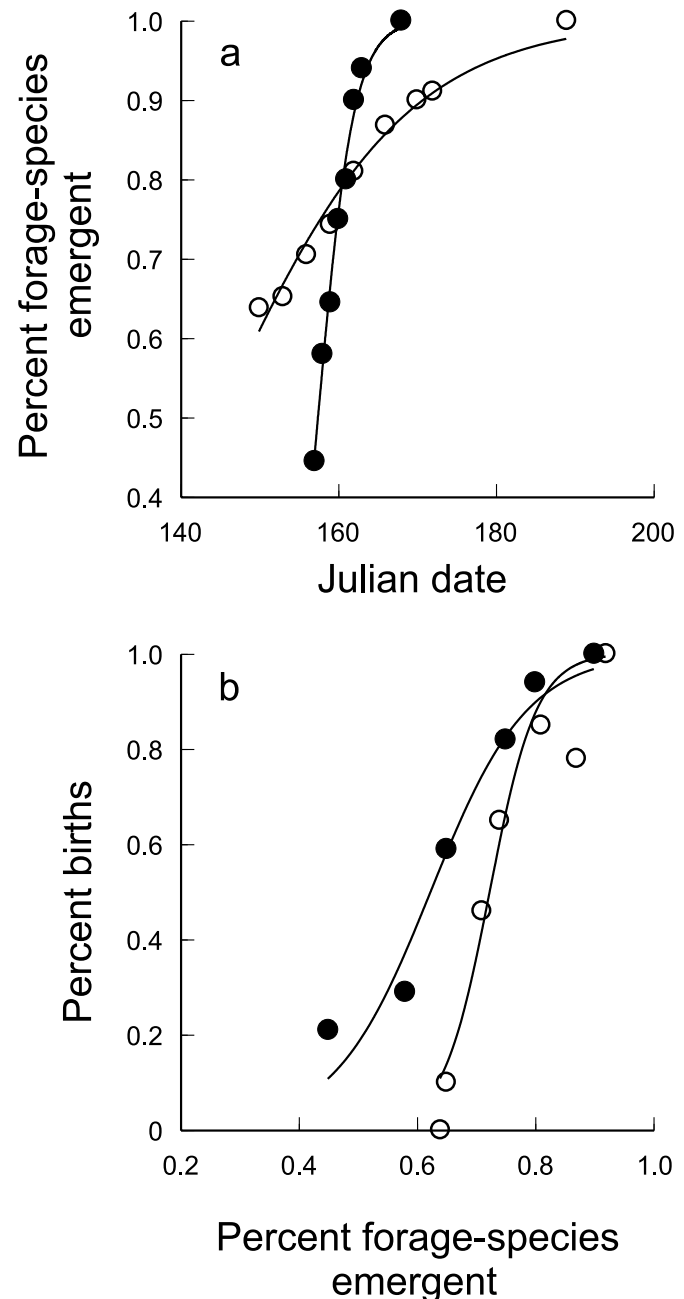
**Fig. 1.** (a) Progression of the caribou (*Rangifer tarandus*) calving seasons expressed as proportion of calves (calves/(cows + calves)) versus Julian date in the Kangerlussuaq-Sisimiut population in West Greenland (gray circles, 1993; black circles, 2002) and in the Caribou River population in Alaska (open circles, 1992). (b) Progression of the caribou calving seasons in the same populations expressed as cumulative percent births versus Julian date (see Materials and methods). The fitted function is  $Y = 1/(1 + e^{-a-bX})$  where  $Y$  is percent births and  $X$  is Julian date.



nous in the KS site even when the data from the two sites were constrained to overlap.

The progression of the calving season in both populations was closely related to the progression of plant phenology in the respective study sites (CR:  $R^2 = 0.93$ ; KS:  $R^2 = 0.96$ ) (Fig. 2b). Despite a significant difference in synchrony of calving between these populations, the slopes of the relationships between the progression of calving and plant pheno-

**Fig. 2.** (a) Progression of plant phenology in the Kangerlussuaq-Sisimiut (●) and Caribou River (○) study sites expressed as the cumulative percent forage-species emergent versus Julian date. Also see Materials and methods. (b) Relationships between the progression of calving (cumulative percent births) and progression of plant phenology (cumulative percent forage-species emergent) in the populations and study sites. The fitted functions are the same as those in Fig. 1. Also see Materials and methods.

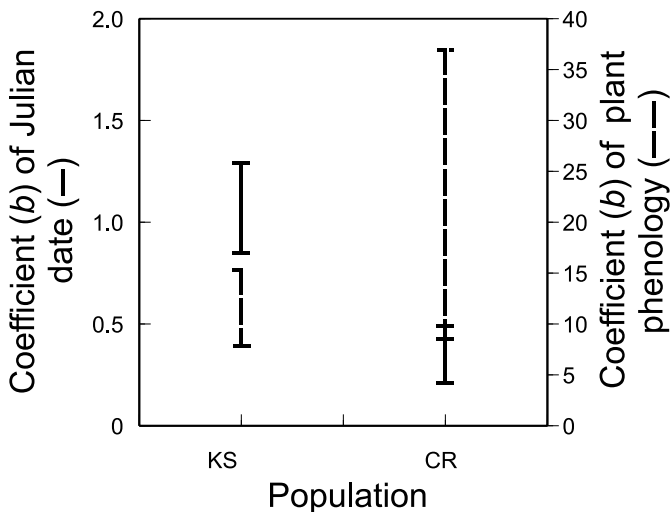


logy in the two populations were statistically indistinguishable (Fig. 3).

## Discussion

Although synchronous parturition certainly reduces the risk of predation to individual offspring born at or near the

**Fig. 3.** Comparison of the coefficients quantifying the relationships between progression of caribou calving and Julian date (solid lines) and between progression of caribou calving and plant phenology (broken lines) in the Kangerlussuaq-Sisimiut (KS) and Caribou River (CR) populations. Bars indicate 95% confidence intervals for the regression coefficients (see Materials and methods).



peak of the season of births (Kruuk 1972; Estes 1977), we concur with Rutberg (1987) that it seems unlikely that synchronous parturition has evolved from an asynchronous state solely in response to predation pressure. Rather, synchrony, a population-level characteristic, must evolve as a consequence of the timing of reproduction by individuals to coincide with a common environmental cue (Rutberg 1987). Our data, and those of other studies (Rachlow and Bowyer 1991; Bowyer et al. 1998), suggest that the degree of synchrony of parturition relates to patterns of plant phenology rather than predation risk.

In a circumpolar comparison of calving times among populations of caribou and wild reindeer that included some with natural predators and some without, Skogland (1989) reported a close agreement between the onset of parturition and the onset of the plant growing season. Skogland (1989) also noted that parturition was more synchronous in northern populations that commenced calving later than in southern populations that calved relatively early and speculated that this difference may have been related to more rapid progression of the plant growing season in northern sites. Our results corroborate those observations.

Calving started later in arctic West Greenland, the more northern of our study sites, and progressed more rapidly (i.e., was more synchronous) there than in our subarctic Alaskan site. This difference apparently reflects disparities in the progression of plant phenology, and the tracking of this phenological progression by female caribou in both populations, because plant growth started later but proceeded more rapidly in Greenland than in Alaska (Fig. 2a). Moreover, de-

spite differences in the progression of calving through time in these two populations (Figs. 1 and 3), the progression of calving in relation to plant phenology was similar in the two areas (Figs. 2b and 3). Previous studies of calving site selection by caribou in North America have also shown that pregnant females track geographic variation in patterns of snowmelt immediately preceding parturition as a means of maximizing intake of highly nutritious, newly emergent forage plants (e.g., Eastland et al. 1989). Such individual-based studies have also shown that selection of calving sites with newly emergent forage plants by preparturient female caribou influences subsequent survival of neonatal calves (Fancy and Whitten 1991).

Early studies of timing of parturition in caribou concluded that the onset of calving was fairly invariant within populations from year to year (Bergerud 1975; Holthe 1975). Our data from West Greenland in 1993 and 2002 display remarkable agreement among years in both the timing and synchrony of parturition in the KS population (Fig. 1a). Without comparable data on plant phenology from West Greenland in 1993, however, it is not possible to determine whether this agreement reflects similar climatic conditions and patterns of plant phenology in those 2 years (i.e., 1993 and 2002). Given the close tracking of plant phenology by caribou evident in this study and others (Skogland 1989; Post and Klein 1999; Van der Wal et al. 2000), it seems plausible that interannual variation in plant phenology, induced, for example, by climatic variability (Post and Stenseth 1999), has the potential to induce variation in the timing of parturition within populations of caribou. Such variation would, undoubtedly, be constrained to some extent by gestation length.

Notably, however, the onset of calving by caribou in Denali National Park, U.S.A., for example, varied by 8 days over a 9-year period (Adams and Dale 1998). This variation matched closely interannual fluctuations in climatic conditions influenced by the Arctic Oscillation (Post 2003). Whether this reflects an indirect influence of climate on timing of parturition acting through plant phenology or a direct influence of climate acting through condition of pregnant females (Adams and Dale 1998) is, however, difficult to determine. Nonetheless, implications of potential climate change for reproductive synchrony in caribou and for synchrony between caribou parturition and plant phenology should be investigated. Of particular interest to us is the question of whether climatic influences on plant phenology may play a role in geographically widespread synchrony in population dynamics of herbivores, exemplified, for instance, by the correlated population dynamics of caribou throughout West Greenland (Post and Forchhammer 2002) and by synchrony among populations of Greenlandic caribou and Russian wild reindeer separated by thousands of kilometres (Post 2004).<sup>2</sup>

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## References

- Adams, L.G., and Dale, B.W. 1998. Reproductive performance of female Alaskan caribou. *J. Wildl. Manag.* **62**: 1184–1195.
- Bergerud, A.T. 1975. The reproductive season of Newfoundland caribou. *Can. J. Zool.* **53**: 1213–1221.
- Bjørnstad, O.N., Falck, W., and Stenseth, N.C. 1995. A geographic gradient in small rodent density fluctuations: a statistical modeling approach. *Proc. R. Soc. Lond. B Biol. Sci.* **262**: 127–133.
- Bøving, P.S., and Post, E. 1997. Vigilance and foraging behaviour of female caribou in relation to predation risk. *Rangifer*, **17**: 55–63.
- Bowyer, R.T. 1991. Timing of parturition and lactation in southern mule deer. *J. Mammal.* **72**: 138–145.
- Bowyer, R.T., Van Ballenberghe, V., and Kie, J.G. 1998. Timing and synchrony of parturition in Alaskan moose: long-term versus proximal effects of climate. *J. Mammal.* **79**: 1332–1344.
- Caughley, G. 1977. Analysis of vertebrate populations. Wiley & Sons, New York.
- Caughley, G., and Caughley, J. 1974. Estimating median date of birth. *J. Wildl. Manag.* **38**: 552–556.
- Darling, F.F. 1938. Bird flocks and breeding cycle. Cambridge University Press, Cambridge, U.K.
- Eastland, W.G., Bowyer, R.T., and Fancy, S.G. 1989. Effects of snow cover on selection of calving sites by caribou. *J. Mammal.* **70**: 824–828.
- Estes, R.D. 1976. The significance of breeding synchrony in the wildebeest. *East Afr. Wildl. J.* **14**: 135–152.
- Estes, R.D., and Estes, R.K. 1979. The birth and survival of wildebeest calves. *Z. Tierpsychol.* **50**: 45–95.
- Fancy, S.G., and Whitten, K.R. 1991. Selection of calving sites by Porcupine herd caribou. *Can. J. Zool.* **69**: 1736–1743.
- Festa-Bianchet, M. 1988. Birthdate and survival in bighorn lambs (*Ovis canadensis*). *J. Zool. (Lond.)*, **214**: 653–661.
- Finney, D.J. 1947. Probit analysis: a statistical treatment of the sigmoidal response curve. Cambridge University Press, Cambridge, U.K.
- Gaillard, J.M., Delorme, D., Jullien, J.M., and Tatin, D. 1993. Timing and synchrony of births in roe deer. *J. Mammal.* **74**: 738–744.
- Holthe, V. 1975. Calving seasons in different populations of wild reindeer in south Norway. *Biol. Pap. Univ. Alaska*, **1**: 194–198.
- Ims, R.A. 1990. On the adaptive significance of reproductive synchrony as a predator-swamping strategy. *Am. Nat.* **136**: 485–498.
- Klein, D.R. 1990. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. *Rangifer Spec. Issue*, **3**: 123–130.
- Klein, D.R., Meldgaard, M., and Fancy, S.G. 1987. Factors determining leg length in *Rangifer tarandus*. *J. Mammal.* **68**: 642–655.
- Kruuk, H. 1972. The spotted hyena: a study of predation and social behavior. University of Chicago Press, Chicago, Ill.
- McGinnis, B.S., and Downing, R.L. 1977. Factors affecting the peak of white-tailed deer fawning in Virginia. *J. Wildl. Manag.* **41**: 715–719.
- Meldgaard, M. 1986. The Greenland caribou — zoogeography, taxonomy, and population dynamics. *Medd. Groenl.* **20**: 1–88.
- Nellemann, C., and Thomsen, M.G. 1994. Terrain ruggedness and caribou forage availability during snowmelt on the arctic coastal plain, Alaska. *Arctic*, **47**: 361–367.
- Post, E. 2003. Timing of reproduction in large mammals: climatic and density-dependent influences. In *Phenology: an integrative environmental science*. Edited by M.D. Schwartz. Kluwer, New York. pp. 437–449.
- Post, E., and Forchhammer, M.C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature (Lond.)*, **420**: 168–171.
- Post, E., and Klein, D.R. 1996. Relationships between graminoid growth form and levels of grazing by caribou (*Rangifer tarandus*) in Alaska. *Oecologia*, **107**: 364–372.
- Post, E., and Klein, D.R. 1999. Caribou calf production and seasonal range quality during a population decline. *J. Wildl. Manag.* **63**: 335–345.
- Post, E., and Stenseth, N.C. 1999. Climatic variability, plant phenology, and northern ungulates. *Ecology*, **80**: 1322–1339.
- Post, E.S. 1995. Comparative foraging ecology and social dynamics of caribou (*Rangifer tarandus*). Ph.D. dissertation, University of Alaska, Fairbanks.
- Rachlow, J.L., and Bowyer, R.T. 1991. Interannual variation in timing and synchrony of parturition in Dall's sheep. *J. Mammal.* **72**: 487–492.
- Reimers, E., Klein, D.R., and Sørungård, R. 1983. Calving time, growth rate, and body size of Norwegian reindeer on different ranges. *Arct. Alp. Res.* **15**: 107–118.
- Rutberg, A.T. 1987. Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *Am. Nat.* **130**: 692–710.
- Sadleir, R.M. 1969. The ecology of reproduction in wild and domesticated mammals. Methuen, London, U.K.
- Sekulic, R. 1978. Seasonality of reproduction in sable antelope. *East Afr. Wildl. J.* **16**: 177–182.
- Skogland, T. 1989. Comparative social organization of wild reindeer in relation to food, mates and predator avoidance. Paul Parey, Berlin.
- SPSS Inc. 1999. SPSS base 10.0 user's guide. SPSS Inc., Chicago, Ill.
- Thing, H. 1984. Feeding ecology of the West Greenland caribou (*Rangifer tarandus groenlandicus*) in the Sisimiut-Kangerlussuaq region. *Dan. Rev. Game Biol.* **12**: 1–53.
- Van der Wal, R., Madan, N., van Lieshout, S., Dormann, C., Langvatn, R., and Albon, S.D. 2000. Trading forage quality for quantity? Plant phenology and patch choice by Svalbard reindeer. *Oecologia*, **123**: 108–115.
- Vistnes, I., and Nellemann, C. 2001. Avoidance of cabins, roads, and power lines by reindeer during calving. *J. Wildl. Manag.* **65**: 915–925.
- Zar, J.H. 1984. Biostatistical analysis. Prentice-Hall Inc., Englewood Cliffs, N.J.