Pregnancy rate as an indicator of nutritional status in *Rangifer*: implications of lactational infertility

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Introduction

Calf production in *Rangifer* spp. is often high, but predation (Bergerud, 1980; Skogland, 1991) or undernutrition (Skogland, 1985) may decrease calf survival and, therefore, recruitment. While food supply has long been recognized as a limiting factor for wild reindeer (*R. tarandus tarandus*) herds in Norway (Reimers, 1982; Reimers *et al.*, 1983; Skogland, 1985; Tyler, 1987), many North American biologists continue to emphasize the role of predators in the population dynamics of barren-ground caribou (*R. t. grantii*/*groenlandicus*) (e.g., Bergerud, 1980; Davis & Valkenburg, 1991). However, studies in Alaska have demonstrated that body condition of female caribou is a determinant of pregnancy rate (Gerhart *et al.*, 1997) and parturition rate (Cameron *et al.*, 1993; Cameron & Ver Hoef, 1994), both of which increase directly with autumn body weight and fatness, as they do in reindeer (Reimers, 1982). A decline in fecundity is manifested as an increased frequency of breeding pauses (Dauphine, 1976; Reimers, 1982; Cameron, 1994).

Probability of pregnancy may also be influenced by lactation status. At the same body weight and fatness, caribou that extend lactation through mid-November are nearly 50% less likely to be pregnant than those that are ceasing lactating (Fig. 1). This condition-unrelated decrease in fecundity appears to be an example of lactational infertility, in which...
suckling delays normal follicular development and ovulation by suppressing gonadotropin (principally luteinizing hormone) secretion (McNeilly, 1994). Here, we investigate the extent to which the proportion of females extending lactation influences the pregnancy rate of a caribou herd.

Methods
Simple population modeling was performed using a spreadsheet. Initial percentages of lactating and nonlactating females were similar to those observed previously in arctic caribou (e.g., Dauphiné, 1976; Cameron et al., 1993). The percentage of females extending lactation was increased from 15 (Year 1) to 70 (Years 2–4), a range similar to that observed in the Porcupine Herd (Gerhart et al., 1997). Pregnancy rates applied to each class of female, after Gerhart et al., (1997), were assumed to be constant. Overall pregnancy rates for the herd were calculated as the weighted means of all classes.

Minimum sample sizes necessary to detect changes in pregnancy rate between years 1 and 4 were calculated according to Zar (1984) (at α=0.05, with 90% power, i.e., β=0.10), assuming equal samples sizes in years 1 and 4.

Results
Output of the model was as follows (Table 1):
In year 1, 85% of adult females in the herd were lactating, of which 15% extended lactation. Given pregnancy rates of 90 and 50%, respectively, for those ceasing and extending lactation, 84% of the lactating females were pregnant after the rut. Adding the nonlactating females

<table>
<thead>
<tr>
<th>Year</th>
<th>Lactation class</th>
<th>% of females in herd (% of lactating females)</th>
<th>Pregnancy rate (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Nonlactating</td>
<td>15 (15)</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Ceasing lactation</td>
<td>72.5 (85)</td>
<td>84</td>
</tr>
<tr>
<td></td>
<td>Extending lactation</td>
<td>12.5 (15)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>85</td>
</tr>
<tr>
<td>2</td>
<td>Nonlactating</td>
<td>15 (15)</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Ceasing lactation</td>
<td>25.5 (30)</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>Extending lactation</td>
<td>59.5 (70)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>66</td>
</tr>
<tr>
<td>3</td>
<td>Nonlactating</td>
<td>34 (34)</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Ceasing lactation</td>
<td>20 (30)</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>Extending lactation</td>
<td>46 (70)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>72</td>
</tr>
<tr>
<td>4</td>
<td>Nonlactating</td>
<td>28 (28)</td>
<td>90</td>
</tr>
<tr>
<td></td>
<td>Ceasing lactation</td>
<td>22 (30)</td>
<td>62</td>
</tr>
<tr>
<td></td>
<td>Extending lactation</td>
<td>50 (70)</td>
<td>–</td>
</tr>
<tr>
<td></td>
<td>Total</td>
<td></td>
<td>70</td>
</tr>
</tbody>
</table>

1 Females that are not lactating in autumn; pregnancy rate 90% (Gerhart et al., 1997).
2 Females that cease lactating by early November; pregnancy rate 90% (Gerhart et al., 1997).
3 Females that extend lactation through mid-November; pregnancy rate 50% (Gerhart et al., 1997).
at a pregnancy rate of 90% yielded a value of 85% for the herd.
In year 2, with an increase to 70% extending lactation, the pregnancy rate of lactating females declined to 62%, resulting in an overall decrease to 66%.
In year 3, extended lactation remained at 70%, but high fecundity of the additional nonlactating females (i.e., those females which failed to become pregnant in Year 2) more than compensated for the lower pregnancy rate of lactating females. Consequently, the herd parturition rate recovered somewhat to 72%.
In year 4 and beyond, the pregnancy rate of lactating females remained at 62%, and that for the herd stabilized at 70%.

Discussion

We suggest that nutrient insufficiency during early lactation is the most important determinant of extended lactation. In red deer, low plane of nutrition during lactation decreased milk yield and calf growth rate, but not maternal body weight (Loudon et al., 1983; White, 1983); instead, suckling frequency was increased and ovulation delayed. In caribou, early growth strongly influenced autumn body weight: birth weight and growth to 3-4 weeks of age accounted for 78.6% of the variation in autumn body weight of wild Porcupine Herd calves (Gerhart, 1995). Caribou are almost entirely reliant upon milk nutrients for growth and maintenance prior to approximately 40 days of age (White & Luick, 1984; Parker et al., 1990); therefore, early growth is directly related to maternal plane of nutrition (and maternal body reserves) during this period (White, 1983).

Lactating arctic caribou are apparently unable to produce enough milk to maximize growth of their calves in some years: both body fat content (Gerhart et al., 1996) and growth rate (Gerhart, 1995) decreased during the insect harassment period. Thus variation in either nutrient availability during early lactation (e.g., timing of snow melt; Eastland, 1991) or intensity or duration of insect harassment (Russell et al., 1993) might affect milk production, and therefore frequency of lactational infertility.

Pregnancy rate determined from females sampled randomly may lead to erroneously high estimates of nutrient availability and an overly optimistic potential for population increase relative to evaluations based on lactating females. For herds of caribou in which both parturition rate and oversummer calf survival are high (e.g., Table 1), most adult females will be lactating in autumn. If the percentage of females extending lactation increases, the pregnancy rate of lactating females will decline, thereby increasing the proportion of nonlactating females present the following summer. Because the latter are highly fecund, they will buffer the decrease in pregnancy rate of the herd, and herd productivity will remain stable.

In contrast, nonlactating females are numerous in herds characterized by low rates of neonatal survival. As a result, pregnancy rates are generally high (Skogland, 1991). If calf survival increases, however, high fecundity may not continue unless summer forage resources permit a lactating female to both provide adequate milk for a calf and gain sufficient weight or fat prior to the breeding season.

Monitoring pregnancy rates to detect changes in nutrition is best accomplished by sampling lactating females because they will be more responsive to changes in nutrient availability: nutrition influences pregnancy rate of lactating caribou both through autumn body condition and lactational infertility. Additionally, such monitoring may be less expensive: differences in pregnancy rate between years 1 and 4 (Table 1) are significant if 45 lactating females are sampled each year, versus 80 females sampled randomly from the herd.

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References


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