Observation of a $p < 10^{-9}$ life-history event: implications of record-late caribou birth on ungulate reproductive ecology and field studies

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Abstract: Life-history traits in temperate ungulates are highly seasonal, with events corresponding to the seasonal availability of resources. An important example is birth date, with later-born individuals typically having reduced survival compared with those born earlier in the season. Ungulates, especially those whose offspring are at their mother's heel soon after birth, are typically born in a narrow window of time in late May–early June. In Newfoundland, mean birth date in caribou (Rangifer tarandus (L., 1758); $n = 1175$) was 31 May. Here, we document a sighting of a caribou calf born ~25 July on Fogo Island, Newfoundland (~55 days after the mean birth date). Calving date was estimated using movement rate of the mother and validated by visual observations of the mother. We discuss the implications of this finding as it pertains to caribou ecology, and suggest that studies of ungulate birth date should ensure that observations are continued well past the initial birth pulse to guarantee that a complete picture of ungulate breeding ecology be maintained.

Key words: birth date, caribou, life history, Newfoundland, Rangifer tarandus, ungulates.

Introduction

For ungulates in seasonal environments, life-history events are strongly tied to specific times of year to make optimal use of resources (Bowyer et al. 1998; Côté and Festa-Bianchet 2001; Cook et al. 2004). Timing of birth is a notable example: early-born juveniles tend to be heavier than late-born juveniles (Clutton-Brock et al. 1987; Adams and Dale 1998; Côté and Festa-Bianchet 2001; Feder et al. 2008). Highly synchronous births optimize the amount of time a female has to use and accumulate energy reserves between birth, weaning, and the rut (Guinness et al. 1978; Clutton-Brock et al. 1987). Ungulates generally exhibit birth pulses, the timing and duration of which can be highly variable (Rutberg 1987). Species inhabiting northern latitudes typically display rigid birth synchrony in spring, with most births occurring in May and June (Table 1; Lent 1974). Two main hypotheses exist to explain the short duration of the birthing season in ungulates, and they do not need to be mutually exclusive. The predator saturation hypothesis suggests that the birth pulse serves to swamp predators and improve survival of young born during the pulse (Estes and Estes 1979). The plant phenology hypothesis suggests that young are born at similar times in spring to maximize forage quality and availability to coincide with the period of energetically costly lactation (Estes and Estes 1979). Individuals born late may be unable to accumulate sufficient reserves to survive the winter and can therefore have reduced survival (Adams and Dale 1998; Côté and Festa-Bianchet 2001; Feder et al. 2008); conversely, being born too early could result in starvation or hypothermia (Clutton-Brock et al. 1982).

It is difficult to determine if a given reproductive interval is a consequence of seasonality or predation reduction (Rutberg 1987; Ims 1990), particularly in ungulates because it can depend on the neonatal security strategy used by the species (e.g., “hider–follower” continuum; Lent 1974; Geist 1981). Follower species have less variation in their timing of birth and adopt a stricter birth synchrony to swamp predators (Estes and Estes 1979; Rutberg 1987). This is less important for hiders because they employ cryptic behaviour to avoid predation and thus show more variation in timing of birth (Rutberg 1987).

As a consequence of predation and plant phenology, we would expect there to be selective pressures to shrink the variation of...
the window of birth dates in ungulates. Furthermore, adherence to this high synchronicity in species closer to the “follower” end of the “hider–follower” spectrum (such as caribou, Rangifer tarandus (L., 1758)) may be maintained to allow mother and young to benefit from spatial strategies (e.g., aggregation on calving grounds) that reduce predation risk (Lent 1974). Suboptimal reproductive timing could result in reduced offspring survival (Green and Rothstein 1993; Feder et al. 2008) with potential demographic consequences to a population depending on overall prevalence (COSEWIC 2014).

For the first time, we describe the latest ever documented birth date for wild Rangifer, Rangifer tarandus. We discuss the implications of this finding on our understanding of caribou reproductive ecology and on studies monitoring birth dates of wild ungulates.

### Materials and methods

#### Study area

The study area was on Fogo Island, Newfoundland, Canada (49°N, 54°W). Natural habitat consists of coniferous and mixed forests of balsam fir (Abies balsamea (L.) Mill.), black spruce (Picea mariana (Mill.) Britton, Sterns & Poggenb.), and white birch (Betula papyrifera Marshall), as well as bogs, lakes, and barren rock. Fogo Island has a humid–continental climate with 1043.1 mm annual mean total precipitation (1981–2010) at the nearest meteorological station at Muggar Harbour (~20 km from the island; Environment and Climate Change Canada 2016).

Presently, caribou populations are in decline across Canada and on a global scale (Festa-Bianchet et al. 2011). In Newfoundland, caribou populations have declined more than 60% in the last 10 years, which has led the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to designate the caribou populations in Newfoundland as “Special Concern” (COSEWIC 2014).

#### Calf observation and age determination

We fitted 15 adult female caribou on Fogo Island with GPS collars (1240 g, GPS 4400M; Lotek Wireless Inc., Newmarket, Ontario, Canada) in April 2016. We located each adult female every 10–15 days from ~1 week prior to the start of calving (mid-May) until late summer (end of August). During routine monitoring of these female caribou, we observed and photographed a collared female with a young (~10 day old) calf on 8 August 2016 (Fig. 1). Initial estimate of calf age was field-assessed based on comparisons with field observations of other calves born during the spring and included calf mobility, colouration, and size. The female had also been located 21 days prior, without a calf. We used Windows Live Photo Gallery 2012 to sharpen the images and reduce noise, as well as to adjust saturation, contrast, and brightness to enhance clarity. Animal handling and capture was conducted in accordance with all governmental and institutional laws and rules and conformed to the guidelines of the Canadian Council on Animal Care, Memorial University of Newfoundland protocol ID No. 16-03-EV.

To determine the birth date of the calf, we used a method for inferring birth and calf survival (DeMars et al. 2013). This method uses adult female step length (as a proxy for movement rate) in a priori models which assume that step length is exponentially distributed and any breaks in the scale parameter of the models (that is, mean step length) indicate birth and offspring loss. We applied the model developed by DeMars et al. (2013) to the GPS data from the collared female to estimate the birth date. The estimated birth date was corroborated by visual observations made on the collared female (e.g., she was observed on 18 July without a calf). To determine the likelihood of a calf being born this late in the season in Newfoundland, we used a known distribution of calf birth dates (n = 1175) from Newfoundland between 1979 and 2012. We fitted this distribution to a negative binomial distribution and calculated a p value to estimate the probability of an event this extreme using R version 3.2.1 (R Core Team 2016). Our data represented count data that were non-normally distributed, therefore we opted to fit these data to a negative binomial (e.g., Poisson–Gamma mixture) distribution. We compared the fit of both the negative binomial distribution that we generated and a Poisson distribution to our data using a Kolmogorov–Smirnov

### Table 1. Distribution of mean (or median in parentheses) birth dates and latest recorded birth date from studies of northern ungulates.

<table>
<thead>
<tr>
<th>Species</th>
<th>Location</th>
<th>Mean or (median) Latest date</th>
<th>Latest recorded birth date (days from mean or (median))</th>
<th>n</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Caribou, Rangifer tarandus</td>
<td>Newfoundland, Canada</td>
<td>31 May (13–21 May)</td>
<td>18 June (9–18)</td>
<td>175</td>
<td>Ellington 2015</td>
</tr>
<tr>
<td>Reindeer, Rangifer tarandus</td>
<td>Finland</td>
<td>18–23 May</td>
<td>28–36</td>
<td>154</td>
<td>Holand et al. 2003</td>
</tr>
<tr>
<td>Red deer, Cervus elaphus</td>
<td>Scotland</td>
<td>31 May–13 June</td>
<td>26 August (25–75)</td>
<td>236</td>
<td>Guinnes et al. 1978</td>
</tr>
<tr>
<td>White-tailed deer, Odocoileus virginianus (Zimmermann, 1780)</td>
<td>Minnesota, USA</td>
<td>26 May</td>
<td>19 June (24)</td>
<td>49</td>
<td>Carstensen et al. 2009</td>
</tr>
<tr>
<td>Roe deer, Capreolus capreolus (L., 1758)</td>
<td>Norway</td>
<td>22 May</td>
<td>4 July (43)</td>
<td>146</td>
<td>Linnell and Andersen 1998</td>
</tr>
<tr>
<td>Roe deer</td>
<td>Norway</td>
<td>22 May</td>
<td>11 June (20)</td>
<td>22</td>
<td>Aanes and Andersen 1996</td>
</tr>
<tr>
<td>Dall’s sheep, Ovis dalli Nelson, 1884</td>
<td>Alaska, USA</td>
<td>(18, 27 May)</td>
<td>27 June (17, 31)</td>
<td>22</td>
<td>Rachlow and Bowyer 1991</td>
</tr>
<tr>
<td>Bighorn sheep, Ovis canadensis Shaw, 1804</td>
<td>Alberta, Canada</td>
<td>7 June</td>
<td>18 July (41)</td>
<td>206</td>
<td>Feder et al. 2008</td>
</tr>
<tr>
<td>Mountain goats, Oreamnos americanus (Blainville, 1816)</td>
<td>Alberta, Canada</td>
<td>28 May (26 May)</td>
<td>3 July (36)</td>
<td>109</td>
<td>Côte and Festa-Bianchet 2001</td>
</tr>
</tbody>
</table>

Note: When twinning or triplet rates were reported, we report n as the number birthing events to reduce pseudoreplication of birth dates in the case of twins.

a Minimum and maximum yearly values between 1987 and 1995.

b Minimum and maximum yearly values between 1971 and 1976.

c The value 17 is for the year 1988, whereas the value 31 is for the year 1989.
test and found that the negative binomial distribution was a better fit to the data ($p = 0.259$) compared with the Poisson ($p < 0.001$).

**Results and discussion**

We estimated that the calf in question was born between 19 July and 3 August. The female was previously seen without a calf on 18 July 2016 in a previous survey, and the calf was relatively mobile, such as being able to follow its mother through thick shrub, on the date of observation (8 August) that precluded the calf being younger than 5 days old. The birth-date model (DeMars et al. 2013) estimated a birth date for this calf of 25 July 2016. The mean birth date for calves in Newfoundland between 1979 and 2013 was 31 May. Yam and Dale 1998, and (c) Holand et al. 2003, compared with (d) the estimated birth date for the late-born calf in the case presented here.

**Fig. 1.** Images of a young (~2 week old) caribou (*Rangifer tarandus*) calf and its mother taken on 8 August 2016. Figure appears in colour on the Web.

**Fig. 2.** Frequency of caribou (*Rangifer tarandus*) calves born ($n = 1175$) relative to mean birth date (~31 May) from 1979 to 2012 in Newfoundland (grey bars; Ellington 2015). Fitted negative binomial distribution plotted in red broken line on the Web (grey broken line in print). Arrows indicate the latest date a caribou calf was born relative to the mean birth date according to findings from (a) Ellington 2015 (the plotted data), (b) Adams and Dale 1998, and (c) Holand et al. 2003, compared with (d) the estimated birth date for the late-born calf in the case presented here.
For personal use only.

Giving birth outside the usual reproductive interval has been shown to be maladaptive (Green and Rothstein 1993; Côté and Festi-Bianchet 2001; Feder et al. 2008; Whiting et al. 2011). Caribou are in decline in many regions, with habitat loss being one of the main factors involved in their decline (Festa-Bianchet et al. 2011). Juvenile survival in ungulates is often highly variable and critical for population growth (Gaillard et al. 1998, 2000). The observation of birth ~2 months following the normal birth period may indicate a wider problem if late births become more prevalent, especially since late-born calves often have lower survival compared with calves born during the main birth pulse (Clutton-Brock et al. 1987; Mysterud et al. 2002; Feder et al. 2008; Whiting et al. 2011). The magnitude of this problem, however, is contingent upon determining the true prevalence of very late births in caribou (and other ungulate) populations. Our observation represents the latest observation of birth in wild Rangifer. This suggests that it is likely an exceedingly rare event; alternately, later investigations throughout the birthing seasons may reveal it to be more prevalent. Beyond calf survival, such a late calving date can have reproductive consequences for the female, as late calving can also reduce future fertility of female ungulates (Clutton-Brock et al. 1987; Cameron et al. 1993), which if determined to exist at a larger scale, may result in long-term effects on the fitness and demography of a population.

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