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Birthdate and survival in bighorn lambs (*Ovis canadensis*)

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(With 2 figures in the text)

The relationship between parturition date and lamb survival was investigated among individually marked bighorn ewes in south-western Alberta, Canada. Lambs were born from 17 May to 21 July. Most births occurred in the first two weeks of the lambing period. Lambs born in May enjoyed greater survival than lambs born in June and July. The viability of lambs born after 10 June was extremely low. Inadequate nutrition is suggested as the cause of greater mortality of late-born lambs. Ewes that give birth late are at an earlier stage of lactation when forage quality declines and may not produce sufficient milk to ensure lamb survival. Their lambs have access to high-quality forage for a shortened period. The proportion of late lambs appeared to be correlated with ewe density in the winter range.

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Introduction

Ungulates inhabiting northern environments reproduce seasonally and the distribution of births tends to be skewed toward the beginning of the parturition season. Most young are born within the first one to three weeks (Bergerud, 1975; Guinness, Gibson & Clutton-Brock, 1978; Bunnell, 1980), but the last parturition can occur up to three months after the first one (Mitchell & Lincoln, 1973; Festa-Bianchet, In press). Late births have been attributed to either failure to conceive at the first oestrous cycle (Bergerud, 1975; Guinness *et al.*, 1978; Bunnell, 1980), or to poor body condition (Mitchell & Lincoln, 1973; Clutton-Brock, Guinness & Albon, 1982; Reimers, Klein & Sorumgard, 1983; Cothran, Chesser, Smith & Johns, 1987).

Northern environments are strongly seasonal, with a short growing season when ungulates have access to high-quality forage, and a long season of dormant vegetation, when protein intake is often below that required for maintenance (Hebert, 1973; White, 1983). It is therefore important that the young be born in time to exploit nutritious forage during the growing season (Geist, 1971; Bunnell, 1982). Lactating females also require access to high-quality forage to produce adequate amounts of milk (Munro, 1962; Butterworth *et al.*, 1968; Arman, Kay, Goodall & Sharman, 1974; Berger, 1979).

Predation pressure on newborns may also select for short parturition seasons. If the young are particularly vulnerable in their first few days of life, temporal clumping of births may swamp the predators. Individuals born outside the peak of parturitions would be more likely to be preyed

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upon. The short calving season of wildebeest (*Connochaetes taurinus*) appears to be dictated by predator avoidance (Estes, 1976), and Bergerud (1975) suggested that caribou (*Rangifer tarandus*) may also benefit from reduced predation through synchronized calving.

The relative importance of predation and forage characteristics may be evaluated by analysis of the timing of death of late-born juveniles. If predation was important, juveniles born after the peak of parturitions should suffer greater mortality in the first few days of life than juveniles born earlier. If synchrony with vegetation phenology was the major selective pressure for the timing of birth, any differential mortality of late-born young should occur mostly at an older age.

Limited data are available on the survival of northern ungulates born at different times of the parturition season. Among red deer (*Cervus elaphus*), mortality was greater for calves born very early and very late (Guinness, Clutton-Brock & Albon, 1978; Clutton-Brock *et al.*, 1982), and mortality of late-born calves increased at high population density (Clutton-Brock, Major, Albon & Guinness, 1987). Reviews of the lambing season of North American mountain sheep (*Ovis canadensis* and *O. dalli*) suggest that timing of birth should be very important for lamb survival (Bunnell, 1982; Thompson & Turner, 1982), but field data are scarce. Here I evaluate the importance of birthdate for survival of bighorn lambs and discuss some of the possible causes of late lambing.

Materials and methods

This study was conducted in 1981–1987 in the Sheep River drainage in south-western Alberta, Canada (50°N, 114°W). Detailed descriptions of the study area and the study population are provided elsewhere (Festa-Bianchet, 1986, 1987). The ewes wintered in foothill habitat, on open south-facing grassy slopes, at elevations of 1420–1740 m, and migrated in May to lambing and summering areas located in the Rocky Mountains, 10–12 km to the west, at 1800–2500 m elevation. Data were collected from ewes individually marked with plastic ear tags. Sheep were captured in a corral trap or with tranquillizing drugs (Festa-Bianchet & Jorgenson, 1985). In 1984–1987, 90% of the ewes in this population were marked. The winter range was regularly searched throughout the year (average of 4·7 searches/month; efficiency in locating marked ewes in October–March: 97%), and the alpine areas were searched from late May to early October (for an average of 38 days/year).

Approximate lambing dates (± 3 days) of over 95% of the parous marked ewes were determined in 1984 and 1985 by searching the lambing areas every 2–3 days and estimating each lamb's age at first sighting (Festa-Bianchet, In press). Searching effort was lower in 1986, and the birthdate of only 18 lambs (47% of those born that year) could be estimated within 3 days. However, for 35 lambs born in 1986 it was possible to estimate whether they were born in May or in June. In 1981–1983, the birthdate of most lambs was not determined, but it was possible to identify the 3 lambs born after 10 June because their mothers had been sighted in early June without lambs, and were next seen in late June accompanied by very young lambs. Lamb survival to 5 months was determined by observing nursing interactions of marked ewes. If a parous ewe was observed not to nurse a lamb, or be followed by one, it was assumed that her lamb had died. Survival to 5 months was monitored because this is the approximate age of weaning (Festa-Bianchet, 1987). Nursing was rare for lambs older than 5 months, and monitoring of survival was mostly dependent upon natural and artificial markings of individual lambs. Fifty lambs of marked ewes were captured and tagged in autumn, 1984–1986. Some unmarked lambs were last recognized as individuals (last recorded suckling from their marked mother) when they were 7–9 months old. Six lambs fell into this category in 1986 and 10 in 1984. Survival of marked lambs from 7 months to 1 year was 100% in 1984 ($n = 16$) and 70% in 1986 ($n = 10$), therefore I assumed that all 10 unrecognizable lambs in 1984 and 4 of the 6 in 1986 survived to 1 year. Survival to 1 year was monitored for all lambs of marked ewes in 1985. In 1986, 3 lambs were killed (1 by hunters, 2 during capture attempts) at 5–6 months of age, and were excluded from the analysis of survival to 1 year.

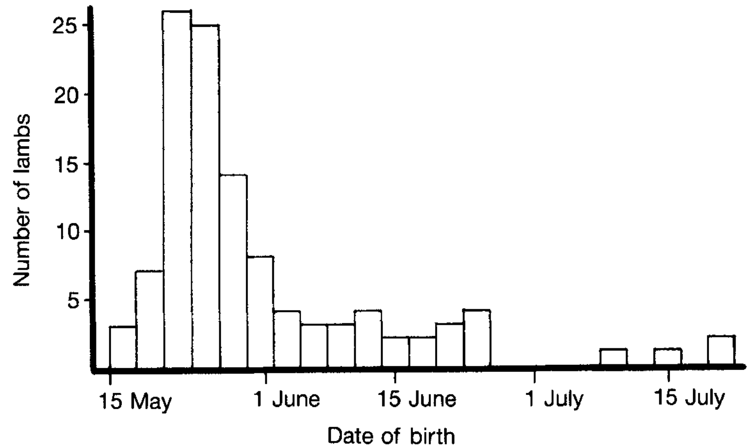

FIG. 1. Estimated birthdates of 112 bighorn lambs at Sheep River, Alberta, in 1984–1986. Bars indicate the number of lambs born every three days beginning on 15 May.

Statistical analyses followed Sokal & Rohlf (1981). Survival of lambs born in May and June–July was compared using *G* tests. The cutoff date of 1 June used for comparisons of surival was chosen because it appeared to be near the end of the 'peak' parturition period (Fig. 1). For correlation analyses, a square-root transformation was applied to lambing dates to approximate a normal distribution. Before the transformation, 15 May was chosen as day 1. The earliest known birth of a bighorn lamb in southern Alberta occurred on 15 May (J. T. Jorgenson, pers. comm.). An arcsine transformation was applied before statistical analysis to all data that are reported as ratios. Two-year-old ewes lamb later than older ewes (Festa-Bianchet, In press), and most analyses were repeated with and without this age class.

Each lamb was treated as an independent datum, even though some lambs were born to the same ewe in different years. The sample analysed included 130 lambs born to 61 ewes in 1984–1986. Fresh groups of faecal pellets were collected in the summer range and analysed for crude protein content with the macro-Kjeldhal acid digestion technique.

Results

Median lambing date was 26 May in 1984 and 1985, and 23 May for the smaller sample obtained in 1986. Lambing extended over 66 days, from 17 May to 21 July, but 71% of the lambs were born in the 15 days from 18 May to 1 June (Fig. 1). There was no between-year difference in the proportion of lambs born in May and June–July ($G = 0{\cdot}74$, $d.f. = 2$, $P > 0{\cdot}5$).

Lambs born in June–July did not suffer greater mortality in their first few days of life than lambs born in May. Survival to two weeks of age was 97% for the former and 96% for the latter. Lambs born in June–July were less likely to survive to five months of age than lambs born in May in 1985 (Table I), and were less likely to survive to one year in 1985 or when data for all years were combined (Table II). Lambs born in May were more likely to survive to one year than lambs born in June–July, also when offspring of two-year-old ewes were removed from the analysis (Table II).

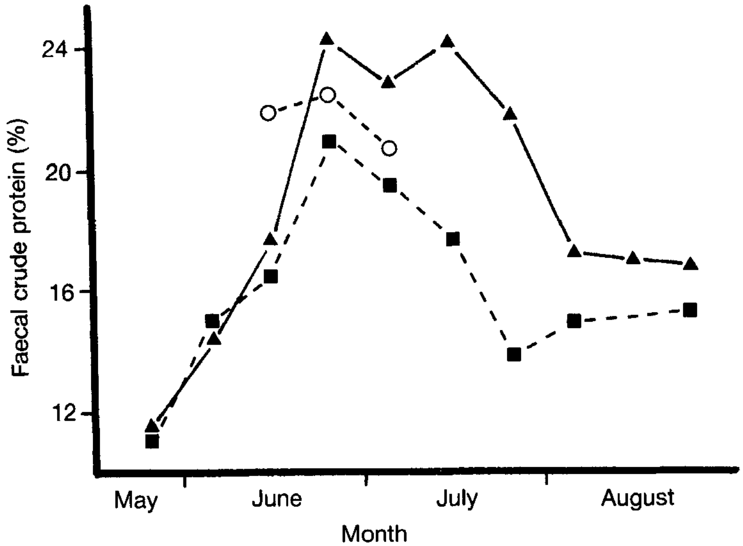

FIG. 2. Percentage crude protein content of bighorn ewe faeces collected in the summer range, averaged every 10 days from 21 May to the end of August, 1984 (▲), 1985 (■) and 1986 (○).

TABLE I

Survival to five months of age of bighorn lambs born in May and in June–July, 1984 to 1986. G-tests are with one degree of freedom

Year	Month of birth	No. lambs	Survival (%)	*G*	*P*
1984	May	37	73	0·99	>0·1
	June–July	9	56		
1985	May	36	56	4·24	<0·05
	July–July	13	23		
1986	May	26	85	0·10	>0·5
	June–July	9	89		
1984–86	May	99	70	3·31	>0·05
	June–July	31	52		

The 20 lambs born on or after 10 June had very low viability: 10 survived to five months, but a maximum of two survived to one year. Of the two survivors, one died at 18 months of age, the other was unmarked and could not be individually recognized after eight months of age (to be conservative, I assumed that this lamb survived to one year). These two were the only lambs born after 10 June that moulted their juvenile coat. The growth of the others appeared to stop at about 5–6 weeks of age and by autumn those that survived appeared frail and emaciated. Their coat was

TABLE II

Survival to one year of bighorn lambs born in May and in June–July, 1984–1986. G-tests are with one degree of freedom

Year	Month of birth	No. lambs	Survival (%)	*G*	*P*
1984	May	37	68	3·50	>0·05
	June–July	9	33		
1985	May	36	19	4·72	<0·05
	July–July	13	0		
1986	May	23	43	3·41	>0·05
	June–July	9	11		
1984–86	May	96	44	10·87	<0·001
	June–July	31	13		
1984–86*	May	94	44	8·57	<0·005
	June–July	19	11		

* Excluding lambs of two-year-old ewes

TABLE III

Proportion of lambs of marked ewes born late (after 10 June), average number of ewes seen in the winter range during searches in the previous October–March period, and adult ram/ewe ratio during the previous rut. Only rams with horns larger than 3/4 curl were included

Year	Late lambs (%)	No. ewes	Ram/ewe ratio
1981	0·0	n/a	n/a
1982	2·8	42	0·32
1983	5·3	75	0·20
1984	10·0	66	0·25
1985	18·0	79	0·26
1986	20·0	83	0·21

matted, dirty and lackluster. Six of the 10 lambs born after 10 June that lived longer than five months were born in 1986, a year when survival to five months of lambs born in June–July was not lower than that of lambs born in May (Table I).

Lambs born in the first six days of the lambing season did not appear to be less viable than other lambs born in May: eight of 10 survived to five months, then one was shot and six of the remaining seven survived to one year.

Forty-one lambs died before their sex could be determined. There was no difference in the sex ratio of lambs born in May (36 males:29 females) and in June–July (16:8) ($G = 0{\cdot}936$, $d.f. = 1$, $P > 0{\cdot}2$). Ewes giving birth in May were older (mean = 6·4 years) than ewes giving birth in June–

July (mean $=4{\cdot}5$ years) (Z transformation of Mann-Whitney U test $=3{\cdot}91$, $P=0{\cdot}0001$). If two-year-old ewes were excluded, however, both groups had the same average age (6·5 years, range 3–12).

Lambing dates of the same ewe in successive years were weakly correlated ($r=0{\cdot}29$, $n=54$, $P=0{\cdot}03$), but not if two-year-old ewes were excluded ($r=0{\cdot}21$, $n=46$, $P=0{\cdot}16$). There was no trend toward earlier or later lambing in successive years among ewes older than two years ($n=46$, paired $t=0{\cdot}18$, $P=0{\cdot}86$). Weaning a son or a daughter had no effect on lambing date the following year (paired t-tests, $P>0{\cdot}3$).

The frequency of lambs born on or after 10 June increased during the study (Table III) ($r=0{\cdot}98$, $n=6$, $P<0{\cdot}01$). Between 1982 and 1986, the proportion of lambs born very late was correlated with the number of ewes in the winter range in the previous October–March period ($r=0{\cdot}81$, $P<0{\cdot}05$), but not with the adult ram/ewe ratio during the previous rut ($r=-0{\cdot}43$, $P=0{\cdot}24$). The crude protein content of ewe faeces in the summer range peaked in late June and early July, then declined (Fig. 2). The protein content of faeces in July was greater in 1984 than in 1985 ($t_{52}=10{\cdot}51$, $P<0{\cdot}001$). Lambs were seen feeding on vegetation from about two weeks of age onward, and by early July they spent about 48% of their active time foraging (Festa-Bianchet, 1987).

Discussion

Lambing at the right time appeared to be very important for the reproductive success of bighorn ewes. Predation soon after birth did not appear to be a major source of lamb mortality, since almost all lambs survived to two weeks of age. It is unlikely that predation pressure on newborns was a major selective force for a short parturition season. Lambs in this population were born in precipitous terrain where they appeared safe from most predators, unlike new-born wildebeest and caribou (Bergerud, 1975; Estes, 1976). Exploitation of high-quality forage for the longest possible time appeared to be the main advantage enjoyed by early-born lambs. The analysis of faecal crude protein suggests that forage quality in the summer range increased with new growth of the vegetation in early June and then declined in late July and August. Therefore, ewes that gave birth late were at an earlier stage of lactation when forage quality declined. Ewes whose lambs were born in June allowed shorter suckles than ewes whose lambs were born in May from the seventh week of lactation onward (Festa-Bianchet, 1987), suggesting that they may have been unable to provide their lambs with sufficient milk. In addition, late-born lambs had access to high-quality forage for a shorter time than lambs born earlier. Research on domestic sheep indicates that forage quality affects the growth of lambs (Slee, 1963; Egan & Doyle, 1982).

The physical appearance of late-born lambs and their mortality pattern suggest that inadequate nutrition was the cause of their lower viability. Crude protein content of faeces was low in the summer of 1985, the only year of the study when lambs born in June–July were significantly less likely to survive to five months of age than lambs born in May. In 1986, eight of nine lambs born in June–July survived to five months of age. The summer of 1986 was very wet and, although measurements were not made, vegetation growth appeared greater than in other years. The following winter was exceptionally mild, with temperatures reaching above freezing almost everyday. It is likely that the favourable forage and weather characteristics of 1986–87 allowed late-born lambs to survive longer than in other years.

The proportion of lambs born after 10 June increased during the study, and was correlated with the number of ewes in the winter range the previous October–March period. Clutton-Brock *et al.*

(1987) reported that among red deer, the average date of parturition was delayed as population density increased. Female ungulates in poor body condition tend to give birth later than other females (Mitchell & Lincoln, 1973; Guinness *et al.*, 1978; Reimers *et al.*, 1983; Cothran *et al.*, 1987). As population density increases, it is possible that fewer resources may be available per capita, and more females may enter the rut in poor condition and conceive later. Because late-born ungulates experience low survival (Clutton-Brock *et al.*, 1987; this study), an increase in late births may act as a form of density-dependent population control.

The ram/ewe ratio during the rut was not related to the frequency of late lambs, and it is unlikely that some ewes failed to conceive in their first oestrus because of unavailability of sexually mature rams. Behavioural observations conducted in 1985 and 1986 indicated that most ewes that appeared to be in oestrus were courted by more than one ram, and given the small size (about 5 km^2) and open habitat of the rutting area, oestrous ewes were unlikely to escape the attention of rams.

Thompson & Turner (1982), reviewing data on the lambing season of northern populations of bighorn sheep, found that, while the initiation of lambing was correlated with the onset of vegetation growth, the end of lambing was not correlated with the length of the growing season. Data presented here suggest that the duration of the lambing period may not be a useful characteristic to compare different populations from an evolutionary viewpoint. Lamb birthdates are not normally distributed, and late births may result from inadequate body condition of some ewes. There is likely to be a strong selective pressure for ewes to lamb early, but environmental factors such as population density and resource abundance can apparently result in lambs being born outside the optimal period. Therefore, without data on lamb survival and the distribution of births, one should proceed with caution before labelling extended lambing seasons as adaptations to, for example, an unpredictable growth season. The occurrence of several late-born lambs may be a sign of resource shortages.

The data collected during this study do not allow us to determine precisely after what lambing date survival becomes significantly lower. This date is likely to vary from year to year, depending on weather and intraspecific competition. The 'best-before' date probably falls between very late May and very early June. After this date, it seems that the later a lamb is born, the lower its chances of survival.

Lambs born after 10 June had an extremely limited chance to survive to reproduce. During this study, only one of 20 (5%) may have done so, and that lamb was born in what superficially appeared to be a year of very favourable weather and forage production. Given that lactation likely entails a cost (Clutton-Brock, Guinness & Albon, 1983; Festa-Bianchet, 1987), it appears that ewes should not breed late, or should abandon lambs born too late. Instead, some ewes bred as late as January and nursed lambs born in July. There may be some exceptionally late growing seasons during which lambs born late may survive, but it is doubtful that these conditions occur very often. If ewes abandoned lambs born very late, or did not breed late in the rut, they may avoid investing in offspring with almost no chance of survival, and save their resources for the next reproductive episode. In the coypu (*Myocastor coypus*), females in good condition can abort small litters early in the season, apparently in order to breed again and conceive larger litters (Gosling, 1986). Among bighorn sheep, abandonment of late-born lambs could be a superior reproductive tactic, but it does not occur. Ewes always respond to stimuli provided by the lamb with milk production and maternal behaviour.

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