EFFECTS OF AGE OF PRIMIPARITY UPON HORN GROWTH IN BIGHORN EWES.

MARCO FESTA-BIANCHET, Département de Biologie, Université de Sherbrooke, Sherbrooke, PQ J1K 2R1, Canada

JON T. JORGENSON, Alberta Fish & Wildlife Services, 5920 1A Street SW, Calgary, AB T2H 0G3, Canada

Abstract: The effects of age of first lambing upon changes in horn length were investigated in a marked population of bighorn sheep (*Ovis canadensis*) in Alberta. Two-year-old ewes that raised a lamb had longer horns at the beginning of the summer (June 5), but grew less horn during summer (June 5 to September 15) than other two-year-old ewes. Horn length of 3-year-olds was independent of age of primiparity.

Several recent studies suggest that animals adjust reproductive effort to reproductive potential (Boyce and Perrins 1987, Pettifor et al. 1988, Stearns 1992, Pettifor 1993;). Age of primiparity (first birth) should largely be determined by variations in individual quality. Individuals that will, on average, profit from early reproduction, should reproduce at a younger age than individuals for whom the fitness costs of early maturation are likely to exceed its benefits.

If this prediction is correct, within a population, individuals that mature early should be of better quality than late-maturing individuals. The post-reproductive growth of early-maturing individuals could be slowed by their investment in reproduction, but not enough to offset the fitness gains of early reproduction. There is, however, little information on the consequences of variation in age of primiparity for subsequent growth of female ungulates. Green and Rothstein (1991) found that bison (*Bison bison*) cows that first calved at 2 years of age were smaller at age 3 than cows giving birth for the first time at 3 or 4 years of age.

In a previous paper (Jorgenson et al. 1993a), we examined the causes of variation in age of first reproduction in bighorn sheep ewes at 2 different study sites. On average, ewes that produced a lamb at 2 years had longer horns as yearlings than ewes who postponed their first lambing until later, but there was considerable overlap in horn length between the two groups. For example, horn length at 15 months of age at Ram Mountain, Alberta varied from 8 to 18 cm (plus a very small ewe with horns of only 4 cm) for ewes that failed to produce lambs at 2 years of age, and from 10 to 18 cm for ewes that produced lambs at 2 years. At Sheep River, Alberta, the horns of 15-month-old ewes that

produced lambs the following year were about 20% longer than the horns of 15-months old that failed to lamb as 2-year-olds (17.3 vs 14.4 cm) (Jorgenson et al. 1993a).

Here, we explore the consequences of variation in age of first reproduction upon subsequent horn growth of bighorn ewes in the Ram Mountain population. We expected less horn growth for ewes that produced and nursed lambs at 2 years of age compared to nonparous ewes of the same age.

STUDY AREA AND METHODS

Ram Mountain (52°N, 115°W, elevation 1082 to 2173 m) is separated from the main Rocky Mountain range by 30 km of coniferous forests. A corral trap baited with salt allowed multiple captures of almost all ewes each year, and over 95% of the population was marked individually in most years. Trapping took place between late May and late September or early October. Horn length was measured with a measuring tape to the closest mm along the front of the horn, from the hairline to the tip. We used the average length of the 2 horns, unless one was

obviously broken, in which case we measured only the most intact horn. If both horns were broken, the ewe was excluded from the sample. The lactation status of ewes was checked at capture by visually inspecting the udder and attempting to squeeze out milk and during observations by noting lamb suckles.

Between 1972 and 1981, the population was kept at 95 – 110 sheep by yearly removal of 12-24% of adult ewes (Jorgenson et al. 1993b). Removals ceased in 1981 and the population increased to 210 sheep by 1992. Only one of 50 2-year-olds produced a lamb during 1989-1991. Therefore, only ewes born before 1987 were considered in our analyses.

Summer horn growth of 2-year-old ewes was approximately linear (Figs. 1 and 2). We adjusted horn lengths to common dates by linear regression with May 25 as day 1. We chose June 5 (day 12) for early-summer horn length, and September 15 (day 114) for late-summer horn length comparisons. We used individual horn growth rates to adjust horn length for ewes with at least 40 days between first and last capture. For ewes caught only once in a summer (6% of ewes), we used an overall regression of horn length on date calculated for all captures of ewes of the same age and reproductive status (barren, lost lamb, or weaned a lamb). Horn length was adjusted only if a measurement was available within 50 days of the desired date; otherwise the ewe was excluded from the sample. The average time between adjusted and measured horn length was 8.8 days ± 0.7 SE for June 5, and 27.4 ± 1.3 days for September 15.

Overwinter horn growth was calculated for individual ewes by subtracting length on September 15 from length on June 5 the following year. More detailed descriptions of our study area and methods are presented elsewhere (Jorgenson et al. 1993a, 1993b).

Definition of Variables

Early producer. A ewe that produced her first lamb at 2 years of age.

Late producer. A ewe not known to produce her first lamb at 2 years.

Successful early producer. An early producer whose lamb survived to early October, the approximate time of weaning.

Statistical Analyses

We used ANOVA to compare three groups of ewes: late producers, early producers whose lamb died, and successful early producers. Sex of lamb reared by 2-year-old ewes had no effect upon maternal mass changes (Bérubé et al. in prep.), therefore data for mothers of lambs of either sex were pooled. ANOVAs were followed by Scheffé tests to detect pairwise differences between the three groups (Sokal and Rohlf 1981). The sample of 2-year-olds that produced but lost their lambs was small; therefore, some comparisons were limited to t-tests between successful early producers and late producers.

RESULTS

Overwinter horn growth of yearling ewes was independent of their reproductive status the following year: it averaged 2.5 ± 0.3 cm for late producers ($n = 40$), 3.0 ± 1.1 cm for unsuccessful early producers ($n = 5$), and 2.8 ± 0.4 cm for successful early producers ($n = 12$) ($F_{2,54} = 0.28$, $P = 0.76$). Early producers already had longer horns as yearlings (Jorgenson et al. 1993a). On June 5 at 2 years of age, successful early producers still had longer horns than late producers ($F_{2,94} = 4.91$, $P = 0.009$, pairwise difference $P<0.05$, Scheffé test). For 2-year-old ewes, horn length and horn growth during summer differed with reproductive status (Fig. 3).

During summer (June 5 to September 15) as 2-year-olds, late producers had greater horn growth (4.1 ± 0.2 cm, $n = 55$) than successful early producers (3.1 ± 0.3 cm, $n = 14$; $t_{41} = 4.52$, $P = 0.001$). The horns of unsuccessful early producers grew considerably (4.4 ± 0.7 cm) but only 3 were captured sufficiently near the beginning and the end of the summer to calculate horn growth, so they were not included in the analysis. Despite greater summer horn growth, by September 15 late producers still appeared to have shorter horns than successful early producers (Fig. 3), although the differences between groups were not significant ($F_{2,79} = 2.81$, $P = 0.07$).

The horns of some 2-year-olds grew between September 15 and June 5, while those of others became shorter. Overall, horn growth over winter was not affected by reproductive status at 2 years ($F_{2,61} = 0.62$, $P = 0.5$), averaging 0.3 ± 0.2 cm. The horns of 3-year-olds on June 5 did not differ according to reproductive status at 2 years ($F_{2,89} = 0.95$, $P = 0.4$), and averaged 20.6 ± 0.3 cm (Fig 3).
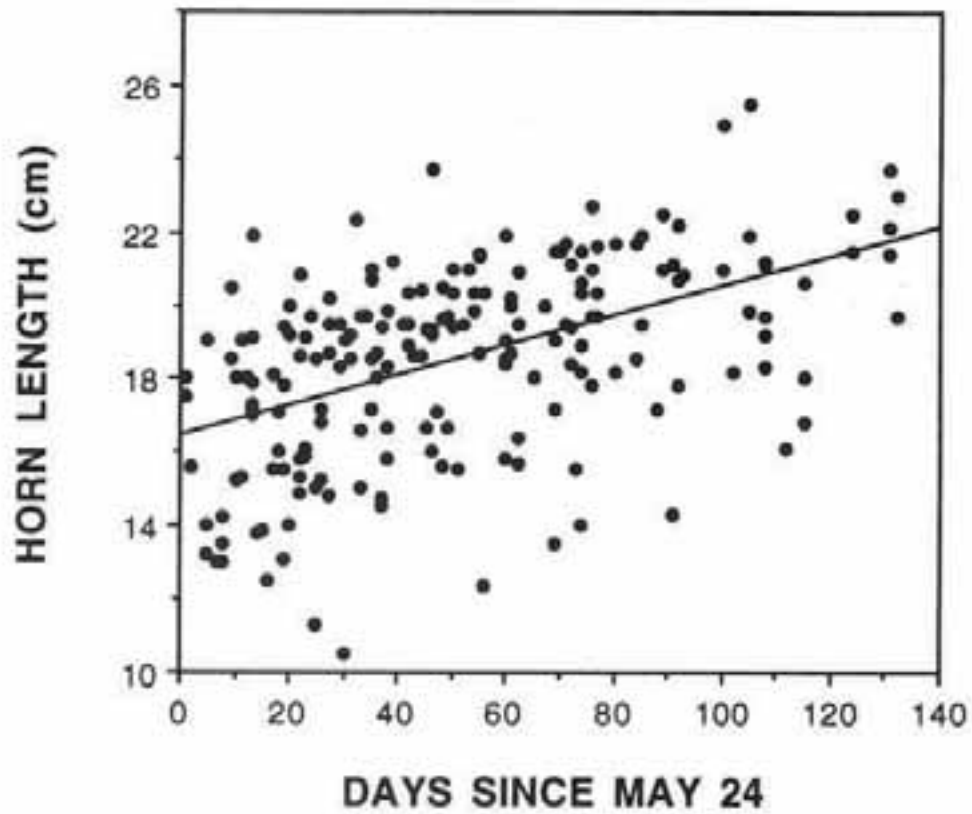
Figure 1. Horn length of all 2-year-old bighorn sheep ewes captured at Ram Mountain, Alberta, 1975 to 1984 ($r^2 = 0.25$).
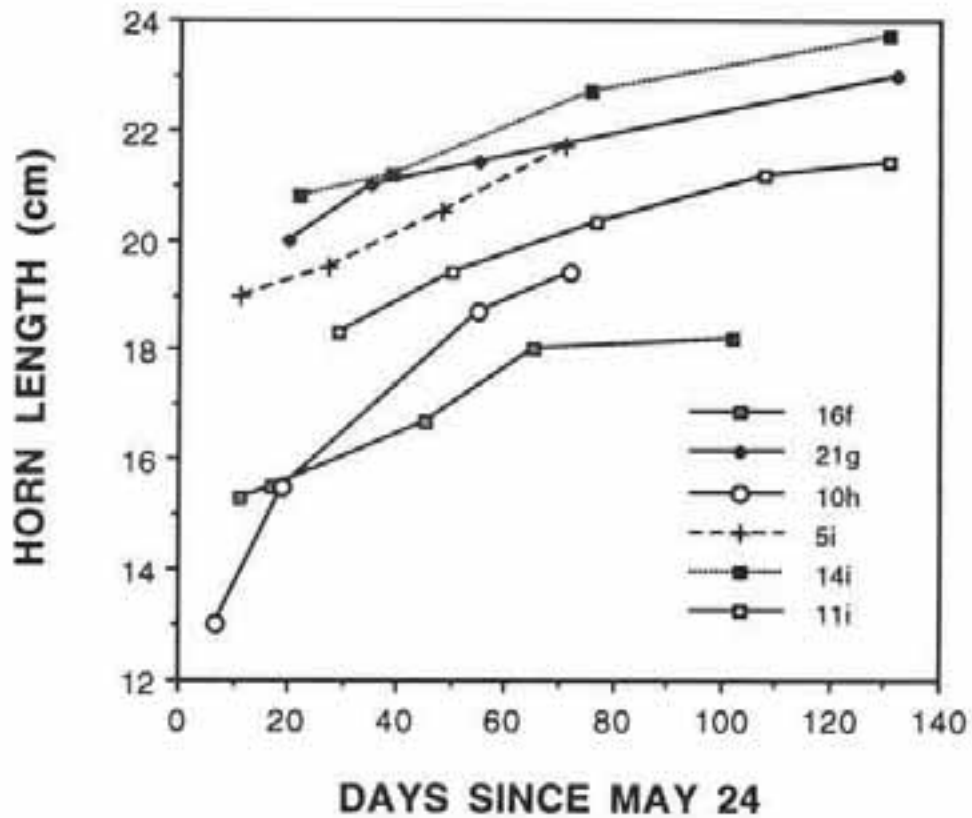

Figure 2. Horn length of individual 2-year-old bighorn sheep ewes captured at Ram Mountain 4 or more times during a summer.
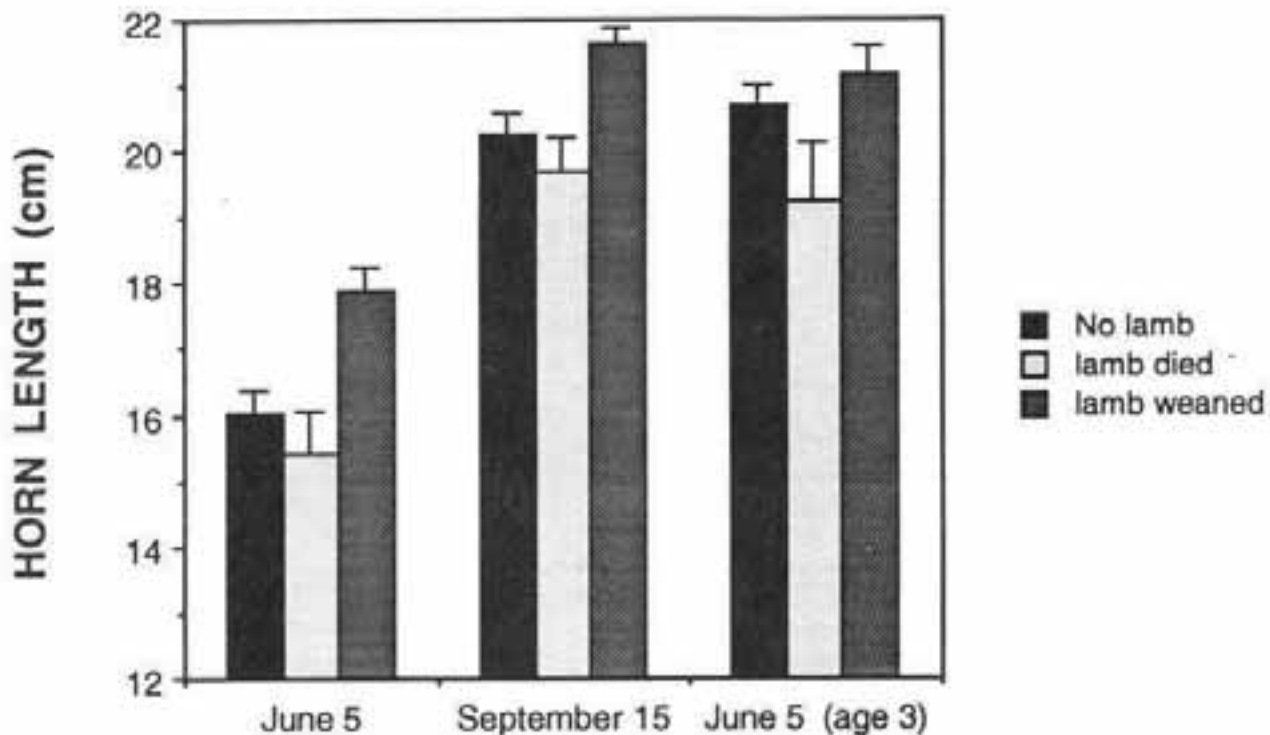
Figure 3. Horn length of 2 and 3-year-old bighorn ewes (x ± SE) of different reproductive status at Ram Mountain, Alberta, 1975 to 1989.

DISCUSSION

We predicted that early reproduction should have negative effects upon horn growth. Horn growth of yearlings between September 15 and June 5 was not affected by pregnancy. This result, however, does not imply that pregnancy had no effects on growth. Horn growth during summer was linear and presumably continued after late September. By the time of the rut in late November or early December, however, ewes had probably either stopped growing their horns or their horn growth rate had considerably diminished. In Dall sheep (Ovis dalli), yearlings cease horn growth by mid-November (Hoefs and Nette 1982), and bighorns likely exhibit a similar pattern because by then they subsist on low-quality forage. Therefore, it is likely that much of the horn growth that we measured between mid-September and early June actually took place between mid-September and December, before any ewes conceived. If our suggestion is correct, then pregnancy could not affect changes in horn length from 1 to 2 years of age.

As expected, horn growth of 2-year-olds nursing lambs through summer was less than for non-

lactating 2-year-olds. This result suggested a short-term trade-off between reproduction and growth: ewes that produced milk were unable to grow their horns at the same rate as non-lactating ewes. Parous 2-year-olds whose lambs died did not bear the costs of lactation. They gained horn length over the summer at a rate similar to that of nonparous 2-year-olds, confirming the negative effect of lactation upon horn growth.

Our results suggest an energetic cost of lactation, which was reflected in lower horn growth. The functions of horns in bighorn sheep females, and in other female bovids (Packer 1983), however, are unclear. It is not known whether a few centimeters difference in horn length may affect a female's life history. Social relationships among females in bighorn sheep appear to have little effect upon reproductive success (Eccles and Shackleton 1986, Festa-Bianchet 1991) and it may be premature to interpret our results as indicators of a long-term life-history cost of early reproduction.

By age 3, age of primiparity had no significant overall effects upon horn length. This finding contrasts with results obtained for body mass in reindeer, Rangifer tarandus, (Leader-Williams and Ricketts 1982) and bison (Green and Rothstein

1991) , where early producers suffered a decrease in body growth. Early reproduction may affect growth in bighorn sheep less than in other ungulates, suggesting that bighorns may recover from the energetic costs of reproduction by exploiting summer forage.

MANAGEMENT IMPLICATIONS

Accurate horn length and horn annuli measurement of bighorn ewes could be useful as an index of the frequency of reproduction among 2-year-olds. In Japanese serow (*Capricornis crispus*), reproduction has a negative effect on female horn growth, and horn annuli reflect a female's reproductive history (Miura et al. 1987). Miura et al. (1987) were able to measure all horn annuli in Japanese serow. In that species, similarly to other rupicaprids, annuli are fairly evident. In bighorn sheep, annuli are difficult to identify for ewes older than 5-6 years. However, an accurate measurement of the first 4 annuli usually is possible. By comparing measurements of the first 3 annuli of different ewes from the same population one should be able to estimate the frequency of early reproduction. This indirect way of assessing reproductive performance would be useful in several ways. For example, it would help in estimating population growth rates and in assessing population status: our study at Ram Mountain revealed that one of the first consequences of increasing population density was an abrupt drop in the frequency of reproduction among 2-year-old ewes (Jorgenson et al. 1993a). It would also be a useful criterion for assessing habitat productivity, as reproduction in 2-year-old ewes is likely indicative of high-quality habitat (Geist 1971).

LITERATURE CITED

Boyce, M. S., and C. M. Perrins. 1987. Optimizing great tit clutch size in a fluctuating environment. Ecology 68:142-153.

Eccles, T. R., and D. M. Shackleton. 1986. Correlates and consequences of social status in female bighorn sheep. Anim. Behav. 34:1392-1401.

Festa-Bianchet, M. 1991. The social system of bighorn sheep: grouping patterns, kinship and female dominance rank. Anim. Behav. 42:71-82.

Geist, V. 1971. Mountain sheep. Chicago: University of Chicago Press. 383 pp.

Green, W. C. H., and A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. Oecologia 86:521-527.

Hoefs, M., and T. Nette. 1982. Horn growth and horn wear in Dall rams and their relevance to management. Bienn Symp. North. Wild Sheep and Goat Counc. 3: 143-156

Jorgenson, J. T., M. Festa-Bianchet, M. Lucherini, and W. D. Wishart. 1993a. Effects of body size, population density and maternal characteristics on age of first reproduction in bighorn ewes. Can. J. Zool. 71:2509-2517.

------, ------, and W. D. Wishart. 1993b. Harvesting bighorn ewes: consequences for population size and trophy ram production. J. Wildl. Manage. 57:429-435.

Leader-Williams, N., and C. Ricketts. 1982. Seasonal and sexual patterns of growth and condition of reindeer introduced into South Georgia. Oikos 38:27-39.

Miura, S., I. Kita, and M. Sugimura. 1987. Horn growth and reproductive history in female Japanese serow. J. Mammal. 68:826-836.

Packer, C. 1983. Sexual dimorphism: the horns of African antelopes. Science 221:1191-1193.

Pettifor, R. A. 1993. Brood-manipulation experiments. I. The number of offspring surviving per nest in blue tits (*Parus caeruleus*). J. Anim. Ecol. 62:131-144.

------, C. M. Perrins, and R. H. McCleery. 1988. Individual optimization of clutch size in great tits. Nature 336:160-162.

Sokal, R. R., and F. J. Rohlf. 1981. Biometry. 2nd ed. Freeman Press, San Francisco. 859 pp.

Stearns, S. C. 1992. The Evolution of Life Histories. Oxford University Press, Oxford. 249 pp.