

Young Bighorn (*Ovis canadensis*) Males: can they Successfully Woo Females?

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Abstract

Mating by young males or low male-to-female ratios can decrease pregnancy rates and postpone birthdates in ungulates, thereby hindering population growth. Young (2.5–3.5 yr old) male bighorn (*Ovis canadensis*) behave differently than older males, and age, horn size, mating behavior, and social rank help determine reproductive success. We estimated birthdates in two populations of bighorn sheep in Utah, USA, to determine if mating by young males or low male-to-female ratios resulted in fewer young born per female, a shift in mean timing of births, or asynchronous births. When reintroduced, the Rock Canyon population consisted of four males (two each of 2.5 yr old and 1.5 yr old) and a 1 to 7.5 ratio of males (>2 yr old) to adult females (≥ 3.5 yr old); the Mount Nebo population consisted of four males ≤ 1.5 yr old and a 0 to 12 ratio of males to adult females. For both populations, the number of young born per female did not differ between the first parturition period after reintroduction (where females were impregnated by males from their source populations) and the second period of parturition (where females were impregnated by young, reintroduced males). Mean birthdates and synchrony (SD) of births did not differ for Rock Canyon (May 12, 2001 \pm 4.5 d, May 14, 2002 \pm 3.2 d) or Mount Nebo (May 23, 2005 \pm 8.1 d, May 22, 2006 \pm 10.2 d) between the first and second years following reintroduction. Mating by young males or low male-to-female ratios had no demonstrable effect on the number of young born per female or timing and synchrony of births in these populations.

Introduction

Mating by young males or a low ratio of males-to-females can reduce pregnancy rates, shift the timing of births (mean birthdate), and protract the synchrony of births (variance around mean birthdate) in some populations of polygynous ungulates. Mating by young, male moose (*Alces alces*) may reduce pregnancy rates (Solberg et al. 2002). Timing of mating is later when young, male fallow deer (*Dama dama*) copulate with females (Komers et al. 1999). In Rocky Mountain elk (*Cervus elaphus nelsoni*), births

are later and less synchronous when younger males breed females (Noyes et al. 1996, 2002). Furthermore, a low ratio of males-to-females may reduce the number of young born in Rocky Mountain elk (White et al. 2001), mule deer (*Odocoileus hemionus*; White et al. 2001), and moose (Aitken & Child 1992; Solberg et al. 2002). Moreover, timing of parturition is later as the male-to-female ratio decreases in reindeer (*Rangifer tarandus*; Holand et al. 2003) and moose (Taquet et al. 1999). Conversely, mating by young males does not influence fecundity in some populations of Rocky Mountain elk (Noyes

et al. 1996, 2002), reindeer (Holand et al. 2003), and moose (Laurian et al. 2000). Presence of young males does not affect timing or synchrony of parturition in reindeer (Holand et al. 2003) or moose (Laurian et al. 2000). A low ratio of males-to-females does not influence number of young born in Rocky Mountain elk (Bender & Miller 1999), moose (Schwartz et al. 1992; Laurian et al. 2000), or reindeer (Holand et al. 2003). Finally, a low ratio of males-to-females may not control the synchrony of parturition in reindeer (Holand et al. 2003). Contradictory evidence abounds for the role of young males in the reproductive biology of female ungulates.

Successful reproduction for male Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) is determined by social interactions, leading to establishment of dominance hierarchies (Geist 1971; Hass & Jenni 1991; Pelletier & Festa-Bianchet 2006). Dominance relationships in bighorn males are evident between 1 and 2 yr of age, with yearling males dominant over most females (Hass & Jenni 1991). Males mature socially with increasing age and weight to prime age (Geist 1968b; Hass & Jenni 1991; Pelletier & Festa-Bianchet 2006). At 3 yr old, males are the same size or slightly larger than females (Festa-Bianchet et al. 1996), and approach asymptotic body size at approx. 6 or 7 yr of age (Blood et al. 1970; Geist 1971; Pelletier & Festa-Bianchet 2006). Social rank, horn size, weight, age, and fighting skills determine mating success (Hogg & Forbes 1997; Coltman et al. 2002; Singer & Zeigenfuss 2002; Pelletier et al. 2004; Pelletier & Festa-Bianchet 2006); and old, mature males obtain a disproportionate number of copulations (Hogg & Forbes 1997; Coltman et al. 2002; Singer & Zeigenfuss 2002).

Young male bighorns behave differently during rut when compared with older males (Geist 1968a, 1971; Hogg 1984; Shackleton 1991; Hogg & Forbes 1997). Young males arrive in rutting areas earlier than older individuals (Geist 1971; Bleich et al. 1997). Moreover, young males use different mating tactics (i.e. coursing or subordinates fight older animals for temporary copulatory access to females defended by the latter). Conversely, older males tend females and block younger males from them, which entails defense and mating over a prolonged period of consort (Geist 1971; Hogg 1984; Shackleton 1991; Hogg & Forbes 1997). Younger males also copulate later than older males that defend females (Hogg 1988). An absence of mature males might result in a less orderly and disruptive mating system, because young bighorn males may harass females excessively (Singer & Zeigenfuss 2002), potentially causing

females to lose body mass (Geist 1971; Komers et al. 1999). In the absence of older conspecifics, however, young bighorn males may possess the necessary mating behaviors to successfully court and mate with females. Conversely, young males may not possess these behaviors, thereby causing a decrease in pregnancy rates and a shift in timing and synchrony of parturition (Deming 1963). A decrease in number of young born can hamper population growth. Delays in births or asynchronous parturition can impede population growth because late-born young suffer higher mortality (Clutton-Brock et al. 1987; Festa-Bianchet 1988a,b; Hass 1997; Keech et al. 2000; Rubin et al. 2000).

In the absence of older individuals, young bighorns are more active during rut (Shackleton 1991; Jorgenson et al. 1997), advance in dominance hierarchies (Hogg et al. 2006), and in some instances young males can inseminate females. In captive populations, 6-mo-old and yearling males may successfully copulate with females (Deming 1963; Blaisdell 1976; Blunt et al. 1976; McCutchen 1976). In small, wild populations, yearling males may also mate successfully (Buechner 1960); however, in large populations yearling males rarely participate in mating, but 2- and 3-yr-old males do so (Hogg & Forbes 1997; Coltman et al. 2002). Nevertheless, whether mating exclusively by young male bighorn sheep, or a low ratio of males-to-females decreases the number of young born or influences the timing and synchrony of births is poorly studied in the wild (McCutchen 1976; Krausman & Bowyer 2003). Few investigators have experimentally tested the effect of male age and male-to-female ratio on these life-history events in ungulates (Noyes et al. 1996, 2002; Mysterud et al. 2002).

Little is known regarding the importance of mating by young males or low ratios of males-to-females in populations of reintroduced animals. From 1923 to 1997, 30 of 100 translocated populations of bighorn sheep throughout their distribution were deemed failures (Singer et al. 2000). Many factors, however, can influence the success of reintroductions (Smith et al. 1991; Singer et al. 2000; Rominger et al. 2004), including the potential influence of male age and the ratio of males-to-females on birth rates and timing and synchrony of births. Indeed, much can be learned to improve reintroduction techniques and thereby enhance successful establishment and perpetuation of populations (Smith et al. 1988, 1991; Valdez & Krausman 1999; Krausman 2000).

Two independent reintroductions of bighorn sheep provided a *post hoc* test of the effect of mating

exclusively by young males (2.5–3.5 yr old) as well as low male-to-female ratios on the number of young born per female and timing and synchrony of parturition. We hypothesized that mating by young males would affect the number of young born per female, delay timing of births, or affect synchrony of births. Moreover, we investigated whether low ratios of males-to-females influenced these same life-history characteristics. We predicted that the number of young born per female would decrease (Aitken & Child 1992; White et al. 2001; Solberg et al. 2002), the peak date of births would be later (Noyes et al. 1996, 2002; Komers et al. 1999; Taquet et al. 1999; Holand et al. 2003), and synchrony of births would be protracted (Noyes et al. 1996, 2002), which might occur if females missed an estrous cycle possibly requiring 15–18 d to return to estrus (Hogg & Forbes 1997).

Methods

Study Areas

We estimated birthdates for two un hunted populations of Rocky Mountain bighorn sheep in Rock Canyon and on Mount Nebo, which are separated by approx. 50 km, in the Uinta National Forest of northern Utah, USA (40°14'N, 111°39'W). Both areas are similar, occupying an extension of the Wasatch Mountains, and are oriented north-to-south with an urban interface to the west. Elevations, which are similar between study areas, ranged from 1388 to 3636 m. We used a climograph, plotting precipitation against temperature, to determine seasons (*sensu* Bowyer et al. 1998; Stewart et al. 2002; Oehler et al. 2003) from the closest weather stations to Rock Canyon (Provo, Utah) from 1980 to 2006 and Mount Nebo (Nephi, Utah) from 1941 to 2006. Four seasons were evident for both areas: spring (March–May), summer (June–September), autumn (October, a transitional month), and winter (November–February).

Generalized zones of vegetation included alpine, conifer, aspen (*Populus tremuloides*), maple (*Acer* spp.), juniper (*Juniperus* spp.), mountain brush, sagebrush (*Artemisia tridentata*), and a grass–forb complex. The latter zone of vegetation was composed of important forage species for bighorn sheep such as bluebunch wheatgrass (*Elymus spicatus*), spike fescue (*Leucopoa kingii*), Sandberg's bluegrass (*Poa secunda*), shortstem buckwheat (*Eriogonum brevicaulis*), and littlecup penstemon (*Penstemon sepalulus*). Plant nomenclature is according to Welsh et al. (1993).

Study Populations

Following capture by personnel of the Utah Division of Wildlife Resources, who held the necessary permits for those activities, sex was determined and age calculated by counting horn annuli (Geist 1966) and evaluating tooth eruption for each bighorn. Females >4 yr old were difficult to age (Geist 1966) and were designated mature (Blood et al. 1970). Females were captured after the mating season to increase the likelihood that they were pregnant. Indeed, in both populations, we estimated birthdates for the young of 88% of the females the spring following reintroduction. Wildlife biologists from the Utah Division of Wildlife Resources exercised care in capturing, handling, and applying radiotransmitting collars (Animal Care and Use Committee 1998).

The reintroduction protocol for bighorn sheep recommends a minimum group of 20 individuals, with males <4 yr old, and a 1 to 3–5 ratio of males-to-females (Douglas and Leslie 1999). Twenty-two individuals were reintroduced to Rock Canyon on January 29, 2001. At release, this group included four males (two each of 2.5 yr old and 1.5 yr old), 15 females (≥ 3.5 yr old), and three neonates (two males and one female). The ratio of males (>2 yr old) to adult females was 1 to 7.5; 10 females were equipped with radio collars. Those reintroduced animals came from the Cadomin area in Alberta, Canada (53°02'N, 117°20'W); in 2002 that population consisted of 847 individuals with 419 males and 428 females (J. Kneteman, pers. comm.).

Eighteen bighorns were captured in Augusta, Montana (47°29'N, 112°23'W), and reintroduced to Mount Nebo on December 31, 2004. This herd consisted of two yearling males, 12 adult females, one yearling female, and three neonates (two males and one female). The ratio of males (>2 yr old) to adult female was 0:12. Ten (one male and nine females) bighorns were equipped with radio collars. Those individuals came from a population that consisted of 287 animals, 50 males, 126 females, 35 neonates, and 76 unclassified individuals in 2004 (Q. Kujala, pers. comm.).

We assumed only young, reintroduced males were mating with females in the two study populations, because they were the only males present. Historically, bighorns occurred in Rock Canyon and on Mount Nebo; however, all indigenous populations of Rocky Mountain bighorn sheep were extirpated by the 1930s in northern Utah (Buechner 1960; Smith et al. 1988). After reintroduction, those populations

used small rutting grounds near the areas of release, and small populations and low number of young males facilitated identifying individuals. Furthermore, all individuals in the Rock Canyon population were marked with blue ear tags. The closest population of bighorn sheep to Rock Canyon was another reintroduced population 14 km to the north; neither old males nor males without ear tags were observed with the Rock Canyon bighorns during observations conducted year-round ($n = 195$, J. C. Whiting, own data). The closest population of sheep to Mount Nebo was the Rock Canyon herd to the north, and no old or unidentified males were observed with the Mount Nebo bighorns during year-round observations ($n = 61$); additionally, in autumn 2006, male and female groups were observed on average twice each week for a total of 33 h during rut (November 3 until December 16), and males from adjacent populations were never seen with bighorns on Mount Nebo.

Estimating Parturition Dates

We relocated both collared and uncollared females from the first week of May to the second week of June each year and counted the number of young born and estimated their parturition dates. During this time, we searched Rock Canyon an average of every 3 d during 2001 and 2002, and Mount Nebo an average of every 5 d during 2005 and 2006. We estimated birthdates based on behavior of females before, during, and after parturition, and the first sighting, motor ability, size, and behaviors of neonates (Festa-Bianchet 1988a,b; Risenhoover & Bailey 1988; Hass 1997). To estimate birthdates of young for uncollared females, we compared their young with neonates of collared females when uncollared and collared females congregated in nursery bands following parturition (Hass 1997; Côté & Festa-Bianchet 2001). The median number of days we back-estimated birthdates was 6 (SD = 5.7 d). We exercised care not to disturb females with young (Animal Care and Use Committee 1998).

Statistical Analyses

We calculated the proportion of young born to the number of adult females each year for both populations and used a Z-test (Remington & Schork 1970) to detect differences in these proportions between the first birthing season (when females were impregnated by mature males from their source populations) and the second birthing season (when females

were impregnated by young, reintroduced males). We used a one-tailed test because we predicted the number of births would decline from the first to the second birthing season. The Z-test accommodates sampling with replacement, which allowed us to collect multiple samples from the same females (Remington & Schork 1970).

Sampling daily was not logistically feasible; hence, we estimated birthdates of young and pooled them into sampling intervals (bins) – the mean sampling interval was 4 d with a standard deviation of 3.8 d. We used equations in Johnson et al. (2004) to calculate corrected mean values (timing of births) and SDs (synchrony of births). These methods were robust to sampling with unequal time intervals, which has not previously been possible, and produced the best estimate of the mean and SD (Johnson et al. 2004). We predicted that the timing of births would be later; therefore, we used a one-tailed *t*-test (Fowler et al. 1998) to examine differences in the mean date of birth (Julian date) for each population between the first and the second birthing seasons. We used this test because it is robust to departures from normality when sample sizes are nearly equal. The SD of the distribution of births is the best estimate of synchronization of births (Johnson et al. 2004). To determine if synchrony of births was different between the first birthing season and the second birthing season, we calculated corrected SDs (Johnson et al. 2004) and used these parameters to calculate coefficients of variation (CV). We then used a Z-test to examine differences in the CVs for each population (Zar 1999).

Results

During the study, we estimated birthdates for 85% of the young born to known adult females in Rock Canyon, and 91% of the young born to known adult females on Mount Nebo. In Rock Canyon, 12 young were born to 14 females in 2001 and 11 young were born to 13 females in 2002, which was not significantly different (Z-test; $Z = 0.074$, $p = 0.47$). On Mount Nebo, 10 young were born to 11 females in 2005 and 11 young were born to 12 females in 2006, which was not significantly different (Z-test; $Z = 0.065$, $p = 0.47$). The range of birthdates for Rock Canyon was 6 to May 23, 2001 and 9 to May 20, 2002; and 7 to May 31, 2005 and May 5 to June 5, 2006 for Mount Nebo. Mean birthdates between 2001 and 2002 did not differ significantly for the Rock Canyon population (*t*-test; $t_{21} = 1.222$,

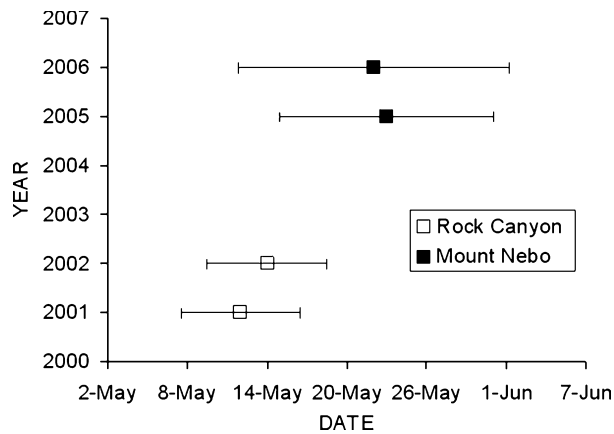


Fig. 1: Mean values (squares) and SDs (horizontal lines) of births for female bighorn sheep in Rock Canyon and Mount Nebo Utah, USA. Young born in 2001 and 2005 were sired by mature males from source populations prior to reintroduction, whereas young born in 2002 and 2006 were sired by young, reintroduced males. Timing (\bar{x} birthdates) and synchrony of births did not differ between the first and second year after reintroduction. Sixty-seven percent of births occurred within ± 1 SD of the mean values.

$p = 0.12$; Fig. 1). Furthermore, mean birthdates between 2005 and 2006 did not differ significantly for the Mount Nebo population (t -test; $t_{19} = 0.247$, $p = 0.40$; Fig. 1). Synchrony of parturition was not significantly different for the Rock Canyon females in 2001 (SD = 4.5 d, CV = 3%) compared with 2002 (SD = 3.2 d, CV = 2%; Z -test; $Z = 0.319$, $p = 0.75$; Fig. 1); likewise, synchrony of parturition did not differ significantly for females in the Mount Nebo population in 2005 (SD = 8.1 d, CV = 6%) compared with 2006 (SD = 10.2 d, CV = 7%; Z -test; $Z = 0.717$, $p = 0.47$; Fig. 1).

There were few seasonal differences and substantial overlap among 95% confidence intervals (CI) between years of study for temperature and precipitation. Overall, there was no between-year variation in annual temperature for Rock Canyon (12°C) or Mount Nebo (11°C). Interannual variation in temperature during spring, when timing of green-up of vegetation might affect timing of births, was negligible for Rock Canyon (Table 1) or Mount Nebo (Table 2). Differences in total annual precipitation were more evident: Rock Canyon (year 1 = 3570 mm, year 2 = 2748 mm) and Mount Nebo (year 1 = 4705 mm, year 2 = 3713 mm). Year 1 received more precipitation during spring than year 2 for both study sites (Tables 1 and 2). Also, the amount of winter precipitation between study areas differed by year (Tables 1 and 2), but the pattern was reversed for the study areas.

Table 1: Seasonal climatic data (mean \pm SD) for Rock Canyon (Provo weather station), Utah, USA, year 1 (June 2000 to May 2001) and year 2 (June 2001 to May 2002)

Season	Year 1		Year 2	
	Precipitation (mm)	Temperature (°C)	Precipitation (mm)	Temperature (°C)
Spring	328 \pm 306	13 \pm 4.7	315 \pm 184.3	11 \pm 5.9
Summer	228 \pm 217.4	23 \pm 3.3	57 \pm 29.3	24 \pm 2.2
Autumn	660	12	148	14
Winter	254 \pm 81	1 \pm 1.5	357 \pm 318.9	2 \pm 3.9

Table 2: Seasonal climatic data (mean \pm SD) for Mount Nebo (Nephi weather station), Utah, USA, year 1 (June 2004 to May 2005) and year 2 (June 2005 to May 2006)

Season	Year 1		Year 2	
	Precipitation (mm)	Temperature (°C)	Precipitation (mm)	Temperature (°C)
Spring	598 \pm 192.3	10 \pm 4.2	467 \pm 354.1	10 \pm 5.7
Summer	129 \pm 83.2	22 \pm 2.4	188 \pm 125.1	21 \pm 4.1
Autumn	773	12	568	11
Winter	406 \pm 189.1	2 \pm 1.5	248 \pm 205.2	1 \pm 2.3

Discussion

Contrary to our predictions, mating by young bighorn males and a low ratio of males-to-females did not decrease the number of young born per female, delay the timing of births, or protract synchrony of births in the populations we studied. Similarly, mating by young males did not influence female fecundity in Rocky Mountain elk (Noyes et al. 1996, 2002), reindeer (Holand et al. 2003), moose (Laurian et al. 2000), or another population of Rocky Mountain bighorn sheep with an age structure skewed toward young males (Shackleton 1991). Those young bighorn males, however, were in the presence of males that were 7.5 yr old (Shackleton 1991). Moreover, young males did not influence timing or synchrony of parturition in reindeer (Holand et al. 2003), moose (Laurian et al. 2000), or other bighorn sheep (Shackleton 1991). Again, those young bighorn males were in the presence of older males (Shackleton 1991). A lower ratio of males-to-females did not affect number of young born in Rocky Mountain elk (Bender & Miller 1999), moose (Schwartz et al. 1992; Laurian et al. 2000), or reindeer (Holand et al. 2003). Also, a low ratio of males-to-females did not influence the synchrony of parturition in reindeer (Holand et al. 2003).

Small populations of bighorn sheep are more susceptible to extinction than larger populations and need enhanced management to increase their probability of persistence (Berger 1990, 1993; Krausman et al. 1993, 1996; Goodson 1994; Wehausen 1999). We estimated birthdates for 88% of fecund females (44 of 50 females) in both populations, nearly a complete count of those animals. In Utah from 1966 to 2006, of 29 reintroductions the average number of animals initially released was 20. Our sample sizes were consistent with those of other populations of reintroduced bighorn sheep. These animals are an ecologically fragile species because of their reliance on fragmented, limited habitats (Risenhoover & Bailey 1988; Bleich et al. 1990; Valdez & Krausman 1999; Singer et al. 2000). Consequently, bighorn sheep are one of the rarest ungulates in North America (Valdez & Krausman 1999); with some populations listed as endangered (Krausman 2000). Reintroductions are the primary way in which biologists, administrators, and conservationists restore populations (Bleich et al. 1990; Krausman 2000). Our results have conservation implications for reintroduced and small populations of bighorn sheep, because they provide preliminary evidence that young males and low male-to-female ratios did not affect the birth rate or timing and synchrony of births.

We documented few differences in timing and synchrony of births in our study populations. Females in Rock Canyon initiated birthing 3 d earlier in 2001 compared with 2002; however, interannual variation in parturition timing >6 d has been reported for Dall's sheep (*Ovis dalli*; Rachlow & Bowyer 1991), red deer (*Cervus elaphus*; Guinness et al. 1978), and bison (*Bison bison*; Berger 1992). Even with a later initiation of births in 2002, the mean birthdate did not differ between 2001 and 2002 for the Rock Canyon population. Furthermore, the distribution of births for the Mount Nebo population was somewhat more clustered in 2005 compared with 2006. The methods of Johnson et al. (2004) accommodate unequal sampling intervals, which differed between years, and the calculated mean birthdates for this population did not differ between 2005 and 2006.

Some mating behaviors in bighorn sheep may be innate; indeed, very young males may exhibit social behaviors involved in courtship and mating (Geist 1968a, 1971; Hogg & Forbes 1997). In the absence of older individuals, young males may possess the necessary behaviors to successfully court and inseminate females. Young bighorn males with greater

access to females become behaviorally mature earlier (Shackleton 1976). Younger males (2.5–4.5 yr old) showed similar mating behavior as older individuals in a population that had a younger age structure of males (Shackleton 1991); however, in that study, males varied in ages from 2.5 to 7.5 yr old, and young males were in the presence of older, dominant males throughout the study (Shackleton 1991). Thus, the presence of older males made it difficult to determine if mating behaviors were innate or learned by younger animals. In our study, younger males were not in the presence of older individuals. Our data provide indirect evidence that young males may have possessed the necessary courtship behaviors because a large proportion of the females gave birth following rut; furthermore, mating by young males did not affect the timing and synchrony of births. We cannot determine, however, if these young males had the full suite of mating behaviors exhibited by older, mature bighorns, or if they harassed females excessively (*sensu* Geist 1971), because we did not quantify mating behavior.

Mating behaviors may be learned from older conspecifics within the first year-and-one-half of life and may be expressed by young animals when larger, mature males are not present. Younger males (2.5–4.5 yr old) showed mating behaviors similar to older individuals (7.5 yr old) in a population that had a younger age structure of males, because of selective harvest of older males by hunting (Shackleton 1991). Nonetheless, young bighorn males in populations with relatively stable age structures usually stay with female groups from birth to 2 yr old (Festa-Bianchet 1991; Ruckstuhl 1998, 1999); as males age from 2 to 4 yr old they gradually switch and spend more time in all-male groups (Festa-Bianchet 1991; Bleich et al. 1997; Ruckstuhl & Festa-Bianchet 2001). The oldest males in the Rock Canyon population were 2.5 yr old at the time of reintroduction and 3.5 yr old at the time of the first mating season. Thus, those males could have associated with old males more so than the males in the Mount Nebo population, which were 1.5 yr old at the time of reintroduction and 2.5 yr old at the time of first mating season. These young, reintroduced males probably spent less time in association with older males and most likely accompanied female groups (Festa-Bianchet 1991; Ruckstuhl 1998, 1999) prior to capture and reintroduction.

Females may have been less selective without mature individuals present (Clutton-Brock et al. 1992). Female fallow deer prefer older males (Clutton-Brock et al. 1989), as do bison (Bowyer

et al. 2007), and female fallow deer can adjust the timing of estrus to be sooner when older males are present (Komers et al. 1999). In populations with older males, female bighorns were more selective, allowing older, dominant males to mate while resisting courtship by younger males (Geist 1968a; Hogg 1984; Hogg & Forbes 1997). Conversely, females that are too selective may miss an estrous cycle, which in female bighorn requires 15–18 d to return to estrus (Hogg & Forbes 1997), possibly resulting in greater variance in birthdates in the presence of young males or at a low ratio of males-to-females, or females may not breed at all (Mysterud et al. 2002). In a captive population of white-tailed deer (*Odocoileus virginianus*), older females thwarted the advances of yearling males, and the sexual advances of those males began as courtship behaviors but ended as aggressive interactions (Ozoga & Verme 1985). Although yearling males behaved differently than older males, and older females were less receptive to their advances, those conditions did not influence the conception rates or timing and synchrony of births (Ozoga & Verme 1985); therefore, indicating that other factors besides male behavior may have been governing timing and synchrony of parturition.

Female ungulates may adjust timing and synchrony of parturition to coincide with the onset of nutritious forage (Bowyer 1991; Rachlow & Bowyer 1991; Berger 1992; Bowyer et al. 1998). For bighorns, births usually occur when suitable temperatures and the abundance of nutritious food favor neonate survival (Bunnell 1982; Thompson & Turner 1982; Festa-Bianchet 1988a; Hass 1997; Rubin et al. 2000). In a population of reintroduced bighorns, one female gave birth 6 mo after the parturition period of other females in that area. The following year that female gave birth in synchrony with the other females, indicating potential plasticity in timing and synchrony of parturition (McCoy et al. 1995). Therefore, we hypothesize that females in our study populations may be dictating timing and synchrony of births regardless of the age of males with which they mate or the ratio of males-to-females. More research on timing of vegetation green-up in relation to births will be necessary to test this hypothesis.

Climatic changes may affect timing and synchrony of births for bighorn sheep through effects of precipitation and temperature on timing of green-up of vegetation (Rachlow & Bowyer 1991). Likewise, interannual differences in forage abundance and quality can affect maternal care and perhaps future

reproduction by females (Rachlow & Bowyer 1994). There were likely few differences in timing of green-up on our study sites because of little interannual variation in temperature. Consequently, temperature was an unlikely cause of minor shifts in timing of births we observed. Interannual variation in precipitation during winter, which typically falls as snow, might explain the slight shifts in dates of birth we observed (e.g. earlier births with less snow; Fig. 1). If young males were primarily responsible for changes in birthdates, we expected a shift to later births. The pattern was mixed between study areas (Tables 1 and 2), indicating that the small changes we observed were more likely related to climate than mating by young males.

Additional studies on captive animals may be necessary to test the influence of male age and the ratio of males-to-females on the number of young born and the timing and synchrony of births (Noyes et al. 1996, 2002; White et al. 2001; Mysterud et al. 2002). Our study of young bighorn males that were reintroduced facilitated a *post hoc* test of whether male age or a low ratio of males-to-females influenced these life-history events in wild populations. A more rigorous experimental test would require manipulation of male age and ratios of males-to-females, which is difficult to achieve with large ungulates (McCullough 1979; Stewart et al. 2005). Our data provide preliminary evidence that in the absence of large males and at low densities, male bighorn sheep as young as 1.5 yr old at the time of reintroduction, and at a low ratio of males-to-females, were able to successfully inseminate females so there was not a decrease in the birth rate. In these systems, we hypothesize that females are adjusting timing and synchrony of parturition around general patterns of onset of nutritious vegetative growth; consequently, mating by young males and the low ratio of males-to-females did not delay the timing of births or protract the synchrony of births.

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