Reintroduced bighorn sheep: do females adjust maternal care to compensate for late-born young?

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Abstract Little is known regarding the potential adjustment of maternal care towards late-born young by reintroduced female ungulates, which may be adapted to environments quite different than those at their release site. We compared nursing behaviors of young to investigate whether females would adjust maternal care toward late-born young between two populations of reintroduced bighorn sheep (*Ovis canadensis*) in Utah, USA. Neonates on Mount Timpanogos were born on average 28 days later in 2002 and 13 days later in 2003 than neonates in Rock Canyon. Suckling and weaning behaviors, however, were similar in 2002 and 2003 between those populations, except for the number of unsuccessful suckles, which was greater for young in Rock Canyon than for young on Mount Timpanogos during the middle of lactation in 2002. Our results provide preliminary evidence that females did not adjust maternal care to compensate for late-born young within the first 3 years following reintroduction, which possibly influenced survivorship of young.

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Introduction

Timing of births and lactation are critical features of mammalian reproduction. For indigenous ungulates occupying seasonal environments in temperate regions, natural selection has likely favored timing and synchrony of births to coincide with suitable environmental conditions, including onset of plant growth (Bowyer et al. 1998; Eastland et al. 1989; Loe et al. 2005; Rutberg 1987); however, exceptions do exist (Bowyer 1991). Young that are born late have less time to garner resources and accumulate body reserves before winter (Bunnell 1982; Festa-Bianchet 1988a; Rachlow and Bowyer 1991; Rubin et al. 2000; Thompson and Turner 1982) and suffer increased mortality to their first winter (Berger 1979; Festa-Bianchet 1988b). Nursing behaviors are essential for the care and social development of young (Millar 1977; Pond 1977; Trivers 1974). Life-history theory predicts that a parent should wean young when the cost of providing milk to young is more demanding than investment in current body condition, survival, and future reproductive potential of the mother (Festa-Bianchet and Jorgenson 1998; Rachlow and Bowyer 1994; Trivers 1974).

Adjustment of maternal care may represent an adaptive response by ungulates to variation in environmental conditions (Berger 1979; Rachlow and Bowyer 1994; Réale et al. 1999). Bighorns born in June nursed for shorter durations than neonates born in May (Festa-Bianchet 1988c). This

reduction in suckling duration occurred for late-born young from 1 month of age onward, because their mothers had access to newly grown forage only during the first month of life of their young. Thereafter until weaning, females fed on forage of declining quality; consequently, mothers were unable to provide young with nutrition sufficient for normal growth and survival (Festa-Bianchet 1988c). In a population of indigenous Dall's sheep (*Ovis dalli*) during a year when the average birthdate for that population was later and births were less synchronous than the previous year, mothers compensated by nursing young for greater total time, reducing time spent nursing sooner, and increasing weaning behaviors in early lactation (Rachlow and Bowyer 1994). Those females adjusted maternal behaviors between years as an adaptive strategy to compensate for late births and variation in environmental conditions (Rachlow and Bowyer 1994). Little is known, however, whether reintroduced females adjust maternal behaviors towards late-born young, especially because females may not adapt immediately to novel environmental conditions (e.g., timing of plant phenology) of their release sites.

The number of ungulate reintroductions has increased dramatically throughout the world (Armstrong and Seddon 2008; Seddon et al. 2007), and analyses of factors associated with successes and failures of reintroductions often are lacking (Griffith et al. 1989; Seddon et al. 2007). From 1923 to 1997, only 41 of 100 populations of bighorns that were translocated throughout the western USA were considered successful (Singer et al. 2000). Many factors can influence the success of bighorn sheep reintroductions (Rominger et al. 2004; Singer et al. 2000; Smith et al. 1991), including potential repercussions for females that do not adjust maternal provisioning for late-born young. Lack of an adjustment of maternal care toward late-born young could hamper population establishment and growth, because mothers may not be able to provide neonates with nutrition sufficient for normal growth (Bunnell 1982; Festa-Bianchet 1988c), and late-born neonates suffer higher mortality than individuals born early (Festa-Bianchet 1988b, c; Hass 1997; Rubin et al. 2000). Additional research is warranted regarding the possible adjustment of behaviors of animals following reintroductions (Seddon et al. 2007).

Our objectives were to study population-level adjustments of maternal behaviors in two adjacent herds of reintroduced Rocky Mountain bighorn sheep. Preliminary data indicated that females on Mount Timpanogos gave birth much later than females in Rock Canyon; therefore, we hypothesized that females on Mount Timpanogos would compensate for late-born young by increasing maternal care for those neonates (sensu Rachlow and Bowyer 1994). We predicted that mothers on Mount Timpanogos would allow late-born neonates to suckle for greater total time in early

lactation compared with young born earlier in Rock Canyon (sensu Rachlow and Bowyer 1994). Furthermore, we predicted that females on Mount Timpanogos with late-born neonates would rebuff the attempts of young to nurse more frequently in early and mid-lactation and terminate suckling bouts more often during early lactation than females in Rock Canyon with early born young (sensu Rachlow and Bowyer 1994). To infer that bighorns were using forage with similar phenological development, we tested for differences in use of elevation by groups of females between populations. Finally, we tested for population-level differences in survivorship of young to their first winter between populations to evaluate fitness consequences of potentially differing maternal behaviors.

Materials and methods

Study areas

All populations of Rocky Mountain bighorn sheep that were indigenous to Utah, USA, were extirpated by the 1960s (Buechner 1960; Smith et al. 1988); hence, there were no indigenous sheep with which to make comparisons. Consequently, we quantified nursing behaviors of neonates of females that were reintroduced on Mount Timpanogos (40°22′N, 111°40′W) and in Rock Canyon (40°15′N, 111°37′W), UT, USA, from 2002 to 2003. These areas were separated by 13 km and consisted of similar habitat because they are an extension of the Wasatch Front Mountains. Elevations in these areas ranged from 1,388 to 3,582 m. From October 2001 to September 2002, 324 mm of precipitation fell, and from October 2002 to September 2003, the area received 346 mm of precipitation (Provo, Brigham Young University, Utah weather station; Western Regional Climate Center). Generalized vegetative zones included alpine, conifer, aspen (*Populus tremuloides*), maple (*Acer* spp.), juniper (*Juniperus scopulorum*), a mountain-brush zone, big sagebrush (*Artemisia tridentata*), and a grass–forb complex. Forage species for bighorns included bluebunch wheatgrass (*Elymus spicatus*), spike fescue (*Leucopoa kingii*), Sandberg's bluegrass (*Poa secunda*), shortstem buckwheat (*Eriogonum brevicaule*), and littlecup penstemon (*Penstemon sepalulus*). Plant nomenclature follows Welsh et al. (1993).

Study populations

Prior to reintroduction, sex was determined, and age was estimated for bighorn sheep by observing patterns of tooth eruption and counting horn annuli (Geist 1966). Females ≥4 years old were designated mature animals. Three groups of bighorn sheep were released on Mount Timpanogos. In

January 2000, 25 animals (six males, 16 females, and three young) were reintroduced from near Rattlesnake Canyon (39°33′N, 110°23′W), UT, USA. In January 2001, two males and eight females were translocated from near Hinton (53°24′N, 117°34′W), Alberta, Canada. In February 2002, two males, six females, and one young were reintroduced from near Sula (45°50′N, 113°59′W), MT, USA. Twenty-two of those females were ≥4 years old at time of release, whereas the average age of the other eight females was 2 years old. Only one reintroduction occurred in Rock Canyon. In January 2001, 22 bighorns—four males, 15 females, and three young—were captured near Hinton, Alberta, Canada, and released near the mouth of Rock Canyon. All females released in Rock Canyon were ≥4 years old. Forty-one individuals were radio instrumented (31 on Mount Timpanogos and 10 in Rock Canyon). Wildlife biologists from the Utah Division of Wildlife Resources held necessary permits for translocating bighorns and used care in capturing, handling, and attaching radio-transmitter collars to bighorns (Gannon et al. 2007). The average number of animals occupying Mount Timpanogos was 37 individuals, whereas the average number of bighorns in Rock Canyon was 38 animals. Females exhibited high pregnancy rates (51 young born to 57 females during our study; Whiting et al. 2008); low population density and high reproductive rates indicate that density-dependent processes (Kie et al. 2003) were not likely to influence maternal care by females in the populations we studied.

Data collection

To estimate dates of parturition and count the number of young born, we relocated collared and uncollared female bighorn sheep from 3 May to 17 July during 2002 and 2003. We searched these areas an average of three times/week. We estimated birthdates of young based on behavior of females before, during, and after parturition. We also used first sighting, motor ability, size, and behavior of neonates to determine age (Festa-Bianchet 1988a, c; Risenhoover and Bailey 1988; Whiting et al. 2008). To estimate birthdates for neonates of uncollared females, we compared their young to neonates of collared females when females congregated in nursery bands after parturition (Côté and Festa-Bianchet 2001; Geist 1971; Hass 1997; Whiting et al. 2008). We exercised care not to disturb females with young (Gannon et al. 2007; Rachlow and Bowyer 1991).

We relocated collared females with young from 20 May to 5 August on Mount Timpanogos and 8 May to 25 August in Rock Canyon to quantify nursing behaviors. We sampled neonate behaviors on Mount Timpanogos on average every 8 days; we visited Rock Canyon on average

every 7 days to conduct sampling. When searching for females with radio collars, we often sighted groups of females without collars. When this occurred, we randomly selected a group, and from that group, we randomly selected a neonate to observe and quantify behaviors using focal-animal sampling (Altmann 1974). If the focal animal was obscured by vegetation or topography, we stopped recording and waited until it came back into view or terminated sampling if it did not do so. We estimated age of young by their size and behavior and by comparing them to known-aged young. We observed nursing behaviors of young during all daylight hours (Berger 1979; Festa-Bianchet 1988c; Green 1986), and we sampled representative age classes of neonates (1 day to 15 weeks old). We observed neonates for a total of 65 h on Mount Timpanogos and 71 h in Rock Canyon. Individual observations of neonates ranged in duration from 0.5 to 7.1 h on Mount Timpanogos and 0.5 to 8.7 h in Rock Canyon. The mean time of observing a neonate on Mount Timpanogos was 2.2 h, whereas the mean observation time of a young in Rock Canyon was 2.5 h.

A suckling bout was successful if the neonate was in contact with the udder of the female for ≥5 s (Festa-Bianchet 1988c; Rachlow and Bowyer 1994; Shackleton and Haywood 1985), otherwise the suckling bout was considered unsuccessful (Rachlow and Bowyer 1994). We used a stopwatch to time duration of suckling bouts to the nearest 1 s, and we recorded whether the neonate or female was responsible for initiation and termination of each suckling bout (Festa-Bianchet 1988c; Rachlow and Bowyer 1994; Réale et al. 1999). Neonates ended suckling bouts by terminating nursing and walking away or changing activity while the mother continued standing (Berger 1979; Green 1990), whereas mothers terminated nursing bouts by lifting their legs, stepping over, or kicking the young and walking away (Berger 1979; Green 1990). During sampling, we also recorded the duration (nearest 1 min) of time spent standing, moving, foraging, and resting by neonates. The rate of successful suckling was summarized on an acts-per-active hour basis (Bowyer and Kitchen 1987; Rachlow and Bowyer 1994). We used this measure because all individuals were not identifiable in these populations (Rachlow and Bowyer 1994). We observed young and females across canyons (a distance >0.6 km) to avoid disturbing these animals.

We recognize that total time spent suckling is an imperfect measure of milk consumption (Berger 1979; Rachlow and Bowyer 1994); moreover, the amount of milk consumed by young differs by sex and age of neonates (Berger 1979; Cameron 1998; Festa-Bianchet 1988c; Hogg et al. 1992). Despite inconsistencies in time spent suckling and milk intake (Cameron 1998; Mendl and Paul 1989; Therrien et al. 2008), weekly means of suckling duration

multiplied by weekly means for rate of suckling, along with weaning behaviors, have been used to document dramatic differences in the amount of maternal care given to young born late at a population-wide level (Rachlow and Bowyer 1994). These measures provide a reliable index to maternal care, are responsive to environmental change, and allow detection of differences in maternal behavior between populations, especially because we sampled most individuals in these small populations. Bighorn mothers aged 2–3 years provide shorter duration of suckles to young than do mature females (Festa-Bianchet 1988c). We quantified suckling behavior for the young of females <4 years old only on three occasions (one bout on Mount Timpanogos and two in Rock Canyon), the remaining samples we collected were from neonates of females >4 years old, and thus age of mothers likely did not influence the measures of maternal care we quantified.

To determine if bighorns in each population were using similar elevations during spring and summer, we relocated collared bighorns as previously described. These observations were imported into ArcView 3.2 (Environmental Systems Research Institute, Redlands, CA, USA) and superimposed onto 1:100,000 US Geological Survey topographical maps. We then overlaid these maps with Digital Elevation Models of 10-m resolution, and each bighorn sheep location was ascribed a value for elevation in meters. We searched areas used by bighorns from 1 October to 31 March (Festa-Bianchet 1988b) to determine the number of young that survived to their first winter. Bighorn sheep are gregarious (Festa-Bianchet 1986; Geist 1971; Ruckstuhl and Festa-Bianchet 2001), and female neonates typically associate with their mothers or other female groups from birth until 6 years old (Festa-Bianchet 1986, 1991), whereas males associate with groups of females from birth until age 2 and a few males until age 4 (Bleich et al. 1997; Ruckstuhl 1998, 1999; Ruckstuhl and Festa-Bianchet 2001). This close association of young to female groups facilitated locating neonates in winter. To document population-wide differences in survivorship of young, we tallied the highest count of young observed during winter (Jorgenson 1992; Roy and Irby 1994) and compared that value with the number of young born in the previous spring to calculate a proportion of neonates that survived to their first winter (Clutton-Brock et al. 1987).

Data analyses

Lack of independence was problematic for comparisons of birthdates between areas, because some neonates were born to the same females across years. Therefore, we estimated birthdates of young and pooled them into sampling intervals to compare distributions of birthdates between populations (Whiting et al. 2008). We used equations in Johnson et al. (2004) to calculate corrected means (timing of births) and SD (synchrony of births). These methods are robust to sampling with unequal intervals (bin sizes) and produce the best estimate of the mean and SD from pooled intervals (Johnson et al. 2004). For statistical comparisons, we used corrected means (Julian date) and standard errors to construct 95% confidence intervals (CIs) to test for differences between timing of births between areas for each year (Whiting et al. 2008). Data regarding timing of births in Rock Canyon during 2002 were modified from Whiting et al. (2008).

We calculated total time spent suckling by young bighorns by multiplying weekly means for duration of successful suckling bouts by weekly means for rate (acts-per-active hour) of suckling (Rachlow and Bowyer 1994). We used regression analysis weighted by sample size (Neter et al. 1990) to analyze weekly means of rate and duration of suckles by study area and year to assure that small samples in some weeks did not bias the fit of regression lines (Rachlow and Bowyer 1994). We used the log10 transformation of total suckling time to satisfy assumptions of equal error variance and nonnormality of error terms (Neter et al. 1990). We used an F-test to compare slopes of regression lines between study areas (Neter et al. 1990). Finally, we compared the ŷ-intercept of regression lines (Neter et al. 1990) between study areas for each year to determine if total suckling time differed between study areas at the beginning of parturition.

We divided the period of lactation into early, middle, and late categories (Rachlow and Bowyer 1994) based on natural breaks in the data at about 3-week intervals. We used the Z-test for proportions with the Bonferroni correction for multiple comparisons (Zar 1999) to examine the number of unsuccessful suckles by neonates, and for number of suckles terminated by females in each study area by year. The Z-test was especially appropriate for our study because this test allows sampling with replacement, and not all of our females could be recognized as individuals. The critical value for the Bonfferoni correction for conducting multiple comparisons was $\alpha=0.008$. We used an F_{max} test to evaluate the assumption of normality (Fowler et al. 1998), and non-normal data were rank transformed prior to analyses (Conover and Iman 1981). We used two-way analysis of variance to investigate relationships for use of elevation by study area, year, and the interaction between study area and year. We investigated pairwise, post hoc comparisons using Tukey–Kramer tests (T). We used a one-way Fisher's exact test (Zar 1999) to investigate the hypothesis that fewer young survived on Mount Timpanogos than in Rock Canyon for each year. Because we predicted that females on Mount Timpanogos would adjust maternal behavior toward late-born young compared with females in Rock Canyon, we employed one-tailed tests to detect

differences between ŷ-intercepts of regression lines, proportion of unsuccessful suckles in early and mid-lacation, and the number of suckles terminated by mothers during early lactation (Rachlow and Bowyer 1994). Furthermore, we used a one-tailed test to detect differences in the number of young surviving to their first winter, because we predicted that late-born neonates on Mount Timpanogos would suffer higher mortality than individuals born early (Festa-Bianchet 1988b, c; Hass 1997; Rubin et al. 2000); all other tests were two-tailed.

Results

We estimated birthdates of 24 neonates on Mount Timpanogos and 23 neonates in Rock Canyon from 2002 to 2003. On average, females on Mount Timpanogos gave birth on 11 June 2002 (95% CI=30 May to 23 June) and 23 May 2003 (95% CI=15 May to 31 May), whereas the mean date of birth for young of females in Rock Canyon was 14 May 2002 (95% CI=12 May to 16 May) and 10 May 2003 (95% CI=6 May to 14 May). Overall, females that were ≥4 years old gave birth to 48 young, whereas females that were <4 years old (n=8 at time of release) gave birth to only three neonates. In 2002, females on Mount Timpanogos gave birth on average 28 days later than females in Rock Canyon. In 2003, females on Mount Timpanogos gave birth on average 13 days later than females in Rock Canyon. For both years, 95% CIs for distribution of births did not overlap.

During observations of maternal groups, the mean number of neonates in a group was 2 (range=1–4) on Mount Timpanogos and 4 (range=1–15) in Rock Canyon. The youngest animal we observed on Mount Timpanogos was 1 day old, and the oldest animal was 60 days old, whereas the youngest animal we recorded behaviors for in Rock Canyon was 3 days old, and the oldest was 103 days old. Suckling behavior was similar between populations within years. In 2002, total suckling time decreased with age of neonates on Mount Timpanogos ($ŷ$=−0.038x+2.79, r^2=0.353, P=0.042) and in Rock Canyon ($ŷ$=−0.027x+2.82, r^2=0.68, P=0.002; Fig. 1). Time spent suckling did not differ between populations at the beginning of parturition (t=0.056, df=19, P=0.261; Fig. 1) and throughout lactation (F=0.69, df=2,19, P=0.515; Fig.1). In 2003, regressions of total time spent suckling on age of neonates were significant for Mount Timpanogos ($ŷ$=−0.019x+2.87, r^2=0.398, P=0.028) and Rock Canyon ($ŷ$=−0.018x+2.744, r^2=0.520, P=0.004; Fig. 1). Total time spent suckling, however, was not different between populations at the beginning of parturition (t=0.256, df=22, P=0.299; Fig. 1) or throughout lactation (F=0.18, df=2,22, P=0.834; Fig. 1).

Weaning behaviors were similar between populations within years. In 2002, proportion of unsuccessful suckles did not differ between areas during early (Z=0.25, P=0.21) and late periods of lactation (Z=0.87, P=0.09); however, young during the middle period of lactation (Z=3.31, P=0.003) in Rock Canyon were less successful at suckling than those on Mount Timpanogos (Fig. 2). Using a critical value of 0.008 from a Bonferroni correction, we observed no differences between study areas for proportion of suckles terminated by females during early (Z=1.98, P=0.012), middle (Z=0, P=1.0), and late periods of lactation (Z=1.74, P=0.021) in 2002. In 2003, proportion of unsuccessful suckles did not differ among early (Z=0.89, P=0.09), middle (Z=0.40, P=0.17), or late (Z=1.23, P=0.06) periods of lactation (Fig. 2). No differences existed between study areas for proportion of suckles terminated by females during early (Z=0.19, P=0.01), middle (Z=0, P=1.0), and late periods of lactation (Z=0, P=1.0) during 2003.

We observed 248 groups of bighorn sheep (122 on Mount Timpanogos and 126 in Rock Canyon) and compared use of elevation between the two populations. Females on Mount Timpanogos used areas with a mean (±SD) elevation of 2,118 m (± 269 m), whereas females in Rock Canyon used areas with a mean elevation of 2,035 m (±158 m). A significant interaction existed for use of elevation (F=4.03, df=1, 244, P=0.05), indicating that use of elevation by females differed between years and study areas. The use of elevation by females did not differ between study areas in 2002 (T=−0.31, P=0.99); however, in 2003, females on Mount Timpanogos used areas on average 139 m higher in elevation compared with females in Rock Canyon (T=−3.02, P=0.01). Females on Mount Timpanogos increased the use of elevation by 85 m in 2003 compared with 2002 (T=2.75, P=0.03); however, females in Rock Canyon used similar elevation in 2002 and 2003 (T=−0.03, P=1.0).

We observed 176 groups of bighorn sheep (93 on Mount Timpanogos and 83 in Rock Canyon) during winter 2002 and 2003 to determine the proportion of young that survived to their first winter for each population. In 2002, fewer young survived to their first winter on Mount Timpanogos (0.67) than in Rock Canyon (1.0; Fisher's exact test; n=26; P=0.05). In 2003, survivorship of young to their first winter did not differ between areas (Mount Timpanogos=0.56 and Rock Canyon=0.81; Fisher's exact test; n=25; P=0.18).

Discussion

In our study, females that gave birth on average 28 days late did not increase time spent suckling within the first 3 years

Fig. 1 Total time spent suckling regressed on age of neonates in two reintroduced populations of bighorn sheep in northern Utah, USA, in 2002 (**a**) and 2003 (**b**). Each point represents total time spent suckling for an individual of a particular age. Total time spent suckling did not differ between populations throughout lactation. Statistics were conducted on log10 transformed data of total suckling time; however, untransformed data are shown for clarity of interpretation
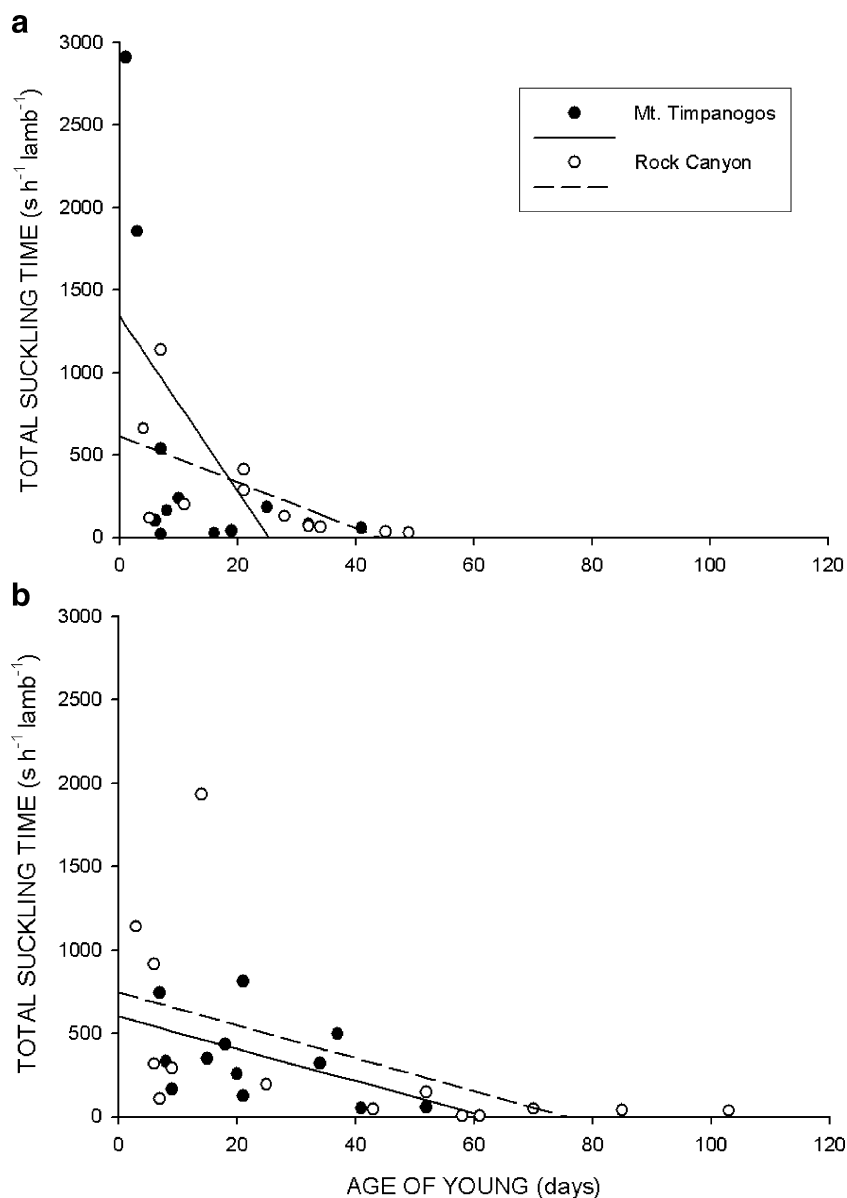
of reintroduction. In contrast, indigenous Dall's sheep that gave birth almost 2 week late, compared with the average birthdate of the previous year, nursed young for greater total time in early lactation (Rachlow and Bowyer 1994). Total time spent suckling was much higher in our study during the first 30 days for both years compared with total suckling time of neonatal Dall's sheep (Rachlow and Bowyer 1994). This dissimilarity in suckling time may occur because female Dall's sheep in that population occur at high densities relative to carrying capacity, occupy areas of high latitudes with severe weather conditions, and potentially reduce investment to young as they rely mostly on endogenous reserves during early lactation (Rachlow and Bowyer 1994). Although total time suckling was high during both years in our study, we predicted that females on Mount Timpanogos would allow late-born neonates to

suckle for greater total time in early lactation compared with young born earlier in Rock Canyon. This adjustment did not occur; therefore, we reject the hypothesis that reintroduced mothers would allow neonates to suckle for greater total time in early lactation to compensate for late births. In one study, young of reintroduced bighorns exhibited different birthing times and suckling behaviors compared with neonates of females from their source herd 22 years after release (Berger 1979). Perhaps in our study areas, with a longer time following reintroduction, either birthdates will synchronize to local conditions or females will adjust maternal care to compensate for late-born young.

Weaning is a gradual process controlled primarily by the mother (Berger 1979; Geist 1971). For young bighorn sheep born in May, weaning probably occurs in September
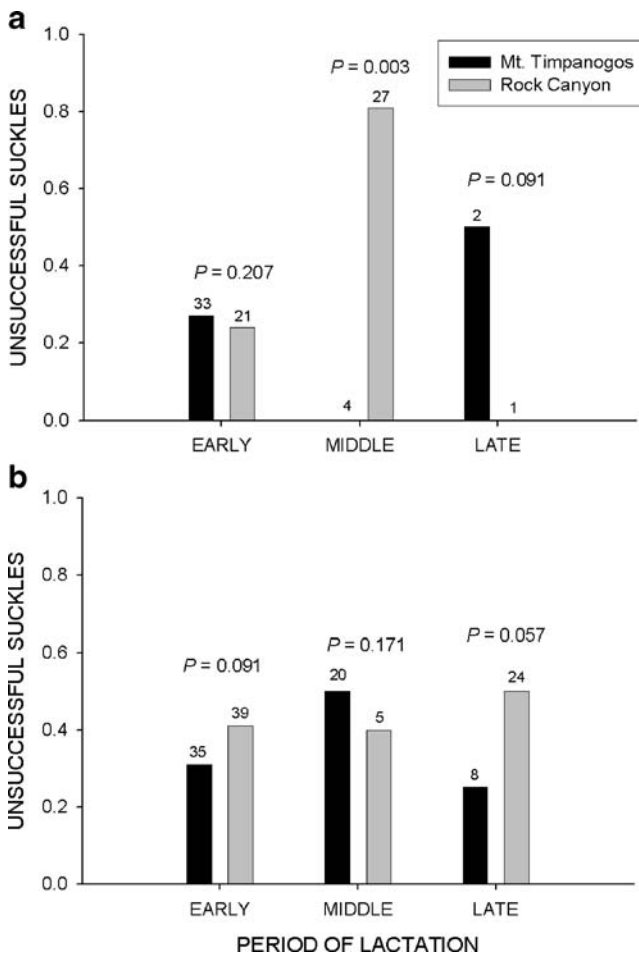
Fig. 2 Proportion of unsuccessful suckles by periods of lactation for neonates in two populations of reintroduced Rocky Mountain bighorns in Northern Utah, USA, from 2002 (a) to 2003 (b). Numbers above bars represent the total number of suckling attempts (unsuccessful and successful) in each period of lactation used to calculate proportions

when forage senesces (Coltman et al. 2005; Festa-Bianchet 1988d; Festa-Bianchet and Jorgenson 1998). Neonatal bighorn sheep cease suckling at 120–150 days after birth, although a few suckling attempts may occur after that time (Festa-Bianchet 1988c). Indigenous Dall's sheep that gave birth almost 2 weeks late, compared with the average birthdate of the previous year, increased the number of unsuccessful attempts to nurse in early and mid-lactation, and terminated suckling bouts more often in early lactation (Rachlow and Bowyer 1994). We predicted that females on Mount Timpanogos with late-born neonates likewise would reject the attempts of young to nurse more frequently in early and mid-lactation and terminate suckling bouts more often during early lactation than females in Rock Canyon. Weaning behaviors, however, were similar between populations in each year, except for the number of unsuccessful suckles during mid-lactation in Rock Canyon in 2002, which was contrary to our prediction, and provided further

evidence that females on Mount Timpanogos did not adjust weaning behaviors to compensate for late-born young.

Potential differences in forage quality and availability to mothers during lactation may influence maternal condition, quality of milk produced, and subsequent care they give to young (Berger 1979; Festa-Bianchet 1988c). Differences in precipitation, temperature, and use of elevation by the bighorn sheep in our study areas may have influenced whether females had access to high-quality forage for longer than mothers that occupied lower elevations. Indeed, forage quality and quantity differ with climate and elevation through differences in snow accumulation (Loe et al. 2005), soil moisture, and plant communities (Douglas 2001), which can produce dissimilarities in phenological development of plants (Berger 1991; Festa-Bianchet 1986, 1988d). In 2002, when birthdates were on average 28 days later on Mount Timpanogos than the average birthdate in Rock Canyon, females used similar elevations between study areas. Those populations were in close proximity (separated by 13 km), and use of elevation by female bighorn sheep differed little between areas during both years. Thus, weather patterns and use of elevation by females between study areas likely did not influence forage quality and availability for mothers.

Plant phenology and thus quality of forage most likely differed throughout lactation for mothers on Mount Timpanogos that gave birth on average 28 days later than females in Rock Canyon. Female bighorn sheep in northern and temperate environments generally give birth before the peak of plant productivity when forage growth and protein content of plants are high (Bunnell 1980; Festa-Bianchet 1988b; Thompson and Turner 1982). Neonates born later suckle from females that feed on forage that is declining in quality and is nutritious for a shorter time than do young that are born earlier than peak productivity of plants (Berger 1979; Bunnell 1982; Festa-Bianchet 1988c; Rachlow and Bowyer 1994). These late-born young also have a shorter time to eat high-quality forage necessary for body growth prior to winter (Bunnell 1982; Festa-Bianchet 1988c). Although we did not quantify differences in plant phenology and quality of forage in our study areas throughout lactation—because we did not want to disturb females with young in small birthing areas—females on Mount Timpanogos that gave birth on average in June likely consumed plants that were later in phenological development and potentially less nutritious than plants eaten by females in Rock Canyon that gave birth in May (Bunnell 1980, 1982; Festa-Bianchet 1988c).

In our study, survivorship of young was most likely influenced by late birthdates and possibly by the lack of adjustment of maternal care towards young. In a population with birthdates of young occurring from May to July, young that were born late suckled for shorter durations and more often (Festa-Bianchet 1988c), ostensibly receiving

less milk than earlier-born young from 1 month of age and onward (Festa-Bianchet 1988b, c). Duration of suckles in early lactation is related to survivorship of young (Festa-Bianchet 1988c), and neonates with low body mass in September suffer lower survival to their first winter (Festa-Bianchet and Jorgenson 1998; Festa-Bianchet et al. 1997). Indeed, young born in May enjoy greater survival than those born in June or July, and survivorship is reduced drastically for young born after 10 June (Festa-Bianchet 1988b). Indeed, maternal condition and subsequent investment in young can influence both size and survival of offspring (Keech et al. 2000; Monteith et al. 2009). On Mount Timpanogos, the average birthdate in 2002 was 11 June; females did not adjust maternal care towards late-born young that suffered reduced survival to their first winter. This lack of adjustment of maternal care may have contributed to reduced survival of those neonates.

Research is needed regarding the behavior of reintroduced animals that are naïve to their surroundings (Griffith et al. 1989; Krausman 2000; Seddon et al. 2007), especially when survival or reproductive rates are low as animals acclimate to conditions of their release site (Armstrong and Seddon 2008). Reintroductions of bighorn sheep have experienced limited success (Rominger et al. 2004; Singer et al. 2000; Smith et al. 1991), and research is needed to improve reintroduction techniques. In our study, females did not adjust maternal care to compensate for late-born young following the first 3 years after release. We hypothesize that this lack of adjustment of maternal care coupled with late birthdates reduced survivorship of young, which could hinder successful establishment of populations of bighorn sheep, and thereby impede the conservation and management of these unique mountain ungulates. We recommend continued monitoring of behaviors of reintroduced animals well after release to determine whether, and how rapidly, animals adjust to conditions of their release site.

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