

Timing and synchrony of births in bighorn sheep: implications for reintroduction and conservation

Jericho C. Whiting^{A,D,G}, Daniel D. Olson^{B,E}, Justin M. Shannon^{B,F}, R. Terry Bowyer^A, Robert W. Klaver^C and Jerran T. Flinders^B

^ADepartment of Biological Sciences, Idaho State University, Pocatello, Idaho 83209-8007, USA.

^BDepartment of Plant and Wildlife Sciences, Brigham Young University, Provo, Utah 84602, USA.

^CUS Geological Survey, Earth Resources Observation and Science Center, Sioux Falls, South Dakota 57198, USA.

^DPresent address: Gonzales-Stoller Surveillance, 120 Technology Drive, Idaho Falls, Idaho 83401, USA.

^EPresent address: Department of Wildland Resources, Utah State University, 375 BNR, 5230 Old Main Hill, Logan, Utah 84322, USA.

^FPresent address: Utah Division of Wildlife Resources, 319 N Carbonville Road, Price, Utah 84501, USA.

^GCorresponding author. Email: jwhiting@gssif.com

Abstract

Context. Timing (mean birthdate) and synchrony (variance around that date) of births can influence survival of young and growth in ungulate populations. Some restored populations of ungulates may not adjust these life-history characteristics to environments of release sites until several years after release, which may influence success of reintroductions.

Aims. We quantified timing and synchrony of births from 2005 to 2007 in four populations of reintroduced bighorn sheep (*Ovis canadensis*) occupying two ecoregions (Central Basin and Range and Wasatch and Uinta Mountains) in Utah, USA, to investigate whether bighorns would adjust these life-history characteristics to environmental conditions of the two ecoregions. We also compared timing and synchrony of births for bighorns in their source herd (Antelope Island) with bighorns in an ecologically similar release site (Stansbury Mountains) during 2006 and 2007.

Methods. We relocated female bighorns to record birthdates of young, and observed groups of collared bighorns to quantify use of elevation by those ungulates. We also calculated the initiation, rate and timing of peak green-up by ecoregion, using the normalised difference vegetation index.

Key results. We quantified 274 birthdates, and although only separated by 57 km, bighorn populations occupying the Central Basin and Range Mountains gave birth an average of 29 days earlier than did those on the Wasatch and Uinta Mountains, which corresponded with the initiation of vegetation green-up. Additionally, bighorn sheep on the Stansbury Mountains (ecologically similar release site) gave birth at similar times as did bighorns on Antelope Island (source area).

Conclusions. Populations of bighorn sheep that were reintroduced into adjacent ecoregions adjusted timing of births to environments and green-up of vegetation in restoration areas. Timing and synchrony of births for reintroduced bighorn sheep in an ecologically similar release site were the same as those of their source area.

Implications. Consideration should be given to the adjustment of timing and synchrony of births when reintroducing bighorns, especially when animals are released into different ecoregions. Also, biologists should select release sites that are ecologically similar to source areas, thereby reducing potential negative effects of animals adjusting timing and synchrony of births to environmental conditions of restoration areas.

Additional keywords: birthing period, *Ovis canadensis*, parturition, restoration, translocation.

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Introduction

In seasonal environments, natural selection has favoured ungulates that adjust timing (mean birthdate) and synchrony (variance around mean birthdate) of births to match favourable climatic conditions (Sadleir 1969; Bunnell 1980; Rutberg 1987) and the onset of nutritious forage (Bowyer 1991; Rachlow and

Bowyer 1991; Loe *et al.* 2005). Neonates that are born late suffer decreased survival to their first winter (Clutton-Brock *et al.* 1987; Festa-Bianchet 1988; Keech *et al.* 2000), reduced survival to yearling age (Guinness *et al.* 1978; Clutton-Brock *et al.* 1987) and decreased future reproductive potential (Reimers *et al.* 1983; Festa-Bianchet *et al.* 2000; Keech *et al.*

2000). Differences in timing and synchrony of births hold important consequences for growth of ungulate populations (Rutberg 1987; Ims 1990; Whiting *et al.* 2011). Furthermore, some restored populations of ungulates may not adjust these life-history characteristics to environments of release sites until several years after being released, which may influence reintroduction success (Marshall and Cambridge 1937; Whiting *et al.* 2011).

Mountain sheep (*Ovis canadensis* and *O. dalli*) occupy areas from northern Alaska to Mexico (Krausman and Bowyer 2003). Timing and synchrony of births for these bovids differ by latitude and elevation (Bunnell 1982; Thompson and Turner 1982). In general, mountain sheep occurring at northern latitudes and higher elevations give birth late in spring, and the birthing period is constricted, which allows females to exploit the shortened growing season (Bunnell 1982; Thompson and Turner 1982). Conversely, mountain sheep that occupy southern latitudes give birth during most months, likely because growing seasons are much less predictable (Lenarz 1979; Thompson and Turner 1982; Rubin *et al.* 2000). Parturition in Rocky Mountain bighorns (*O. c. anadensis*) usually occurs when favourable temperatures and onset of nutritious forage are most conducive for lactation and, thus, survival of neonates (Bunnell 1982; Festa-Bianchet 1988; Hass 1997).

Populations of bighorn sheep have declined substantially since the latter part of the 19th century, and these ungulates face a precarious future (Buechner 1960; Geist 1971; Krausman 2000). Since the 1920s, considerable effort has been exerted and money spent to restore populations of bighorn sheep into historic ranges (Bleich *et al.* 1990; Krausman 2000). Despite those efforts, from 1923 to 1997, only 41% of translocated populations of bighorns were deemed successful (Singer *et al.* 2000). However, little information exists regarding how the behaviour of released ungulates influences the success of reintroductions (Seddon *et al.* 2007). Indeed, understanding the behaviour and life-history characteristics of reintroduced animals that are naïve to their surroundings is critical for successful reintroductions (Griffith *et al.* 1989; Seddon *et al.* 2007), especially in cases when survival or reproductive rates are low as animals become accustomed to conditions of their release site (Armstrong and Seddon 2008; Whiting *et al.* 2011).

Recent work has documented the importance of timing and synchrony of births in bighorn sheep and how differences in these life-history events may influence the success of reintroductions (Whiting *et al.* 2011). Furthermore, ideas regarding ecological similarity (i.e. releasing animals in restoration sites that have similar environmental conditions as source areas; Lawrence and Kaye 2011; Noël *et al.* 2011) have rarely been applied to ungulate reintroductions. We quantified timing and synchrony of births from 2005 to 2007 in four populations of reintroduced bighorn sheep occupying two ecoregions (Central Basin and Range and the Wasatch and Uinta Mountains) in Utah, USA, to investigate whether those bighorns would adjust life-history events to environmental conditions of the two ecoregions. We also tested for differences in the use of elevation by bighorns; and the initiation, rate and timing of peak green-up of vegetation between ecoregions. Additionally, we compared timing and synchrony of births in two populations in which the

environment and habitat were ecologically similar between source (Antelope Island) and release (Stansbury Mountains) sites. We hypothesised that bighorns from an ecologically similar release area would have timing and synchrony of births comparable to those of females from their source area. Our results will provide information regarding adjustment of timing and synchrony of births in reintroduced bighorn sheep, and how matching ecologically similar release sites with source areas can improve the establishment of populations and enhance restoration efforts.

Materials and methods

We estimated birthdates in five reintroduced populations of bighorn sheep occupying two ecoregions in Utah (Central Basin and Range and the Wasatch and Uinta Mountains; Fig. 1; http://www.epa.gov/wed/pages/ecoregions/level_iii_iv.htm#Level%20, verified 12 July 2011). Populations of bighorns in the Central Basin and Range Mountains occupied the Newfoundland Mountains, Antelope Island State Park and the Stansbury Mountains (Fig. 1). The Newfoundland Mountains are located in the Great Salt Lake Desert. The highest peak of that mountain range is 2135 m. Major habitat types are juniper (*Juniperus* spp.), mountain brush, big sagebrush (*Artemisia tridentata* ssp.), sagebrush–grassland and salt-desert shrub. Antelope Island is the largest island of the Great Salt Lake, comprising 11 300 ha (Whiting *et al.* 2009a, 2009b). The island is 24 km long and 8.3 km wide, with the highest peak at 2134 m (Whiting *et al.* 2010a). Habitat types of the island vary from juniper to mountain brush and big sagebrush–grass complex (Whiting *et al.* 2009a). The Stansbury Mountains are located south-west of Antelope Island (Fig. 1). The highest mountain of this range is Deseret Peak at 3362 m. This mountain range is characterised by alpine, conifer, aspen (*Populus tremuloides*), maple (*Acer* spp.), juniper, mountain brush and big sagebrush–grass complex habitats (Olson *et al.* 2008). Weather patterns for these areas are similar (Table 1).

Our other study areas were located along the Wasatch and Uinta Mountains on Mount Timpanogos and in Rock Canyon (Fig. 1). The highest mountain of these two areas reaches 3582 m. These areas are similar in topography and flora, because they are adjacent to and are an extension of the Wasatch Range (Whiting *et al.* 2008, 2011). Generalised vegetative zones descending in elevation include alpine, conifer, aspen, maple, juniper, mountain brush and big sagebrush–grass complex (Whiting *et al.* 2008, 2010b). Weather patterns of these areas also are similar (Table 1).

Although bighorn sheep released in the Central Basin and Range Mountains are considered California bighorns (*O. c. californiana*), recent morphometric evidence indicated that Rocky Mountain and California bighorns should be considered similar subspecies (Wehausen and Ramey 2000). Therefore, we considered all populations in our study areas to be Rocky Mountain bighorns. All indigenous populations of Rocky Mountain bighorn sheep were extirpated in northern Utah by the 1930s (Smith *et al.* 1988). Consequently, from 1996 to 2006, 206 Rocky Mountain bighorn sheep were reintroduced into our study areas (Table 2). In 2007, an additional 48 bighorns were released on Mount Timpanogos and in Rock Canyon; however,

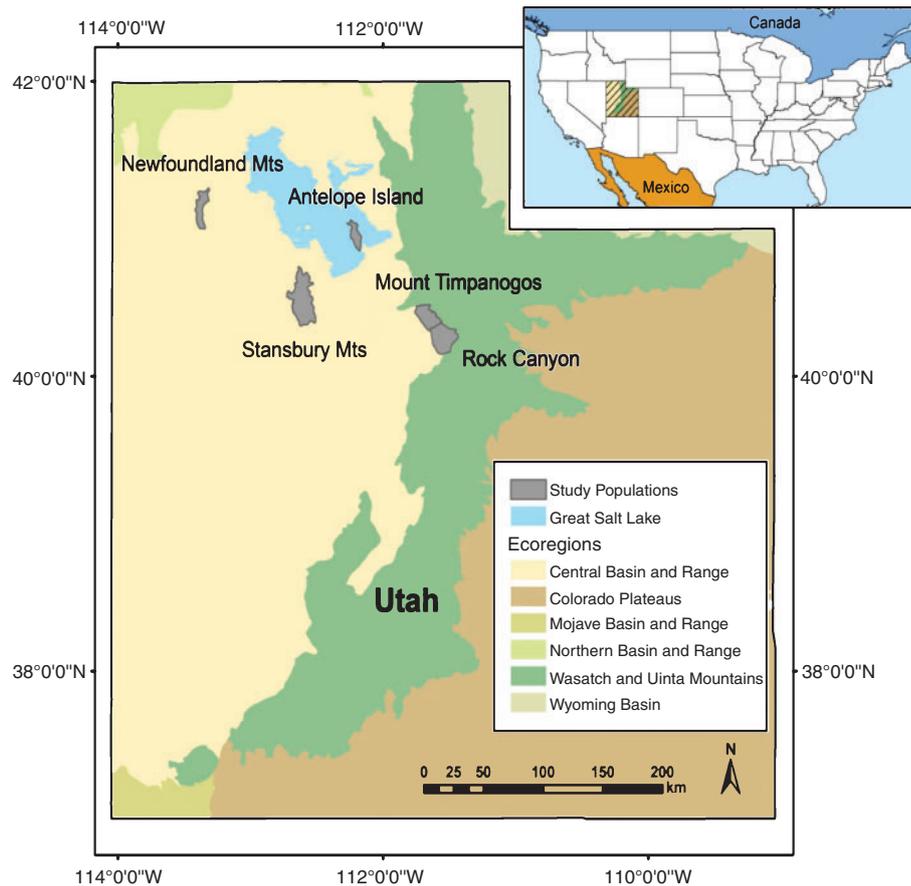


Fig. 1. Study areas and ecoregions in Utah, USA, where we quantified timing and synchrony of births in populations of reintroduced bighorn sheep from 2005 to 2007.

Table 1. Study areas, names of weather stations near areas occupied by bighorn sheep, and the number of years data were collected at those stations; as well as average, yearly climatic information for mountain ranges where bighorns were reintroduced in Utah, USA

All weather data were retrieved online at <http://www.wrcc.dri.edu/index.html>, verified 18 November 2011

Study area	Weather station	Years monitored	Mean max. temperature (°C)	Mean min. temperature (°C)	Total precipitation (mm)	Total snowfall (mm)
Central Basin and Range						
Newfoundland Mountains	Utah Test Range	1989–2008 ^A	18	3	255	409
Antelope Island	Antelope Island	1952–1972 ^A	19	3	393	264
Stansbury Mountains	Callister Ranch	1967–1984 ^A	18	2	325	850
Wasatch and Uinta Mountains						
Mount Timpanogos	Pleasant Grove	1946–2010	18	3	426	1094
Rock Canyon	Provo, BYU	1916–2010	18	4	502	1501

^AWeather stations collected data only during a limited number of years, as indicated.

we did not include any of those females in our analyses of birthdates, because females had not been in release areas for sufficient time (~4 years) to potentially adjust timing and synchrony of births (Whiting *et al.* 2011). Further, we excluded those females in our analyses when we quantified the use of elevation, unless they were with groups of bighorns from previous releases. During our study, the mean (\pm s.d.) number of female bighorns in populations occupying the Central Basin and Range Mountains was 47 ± 16.7 , whereas

15 ± 3.6 females occupied the populations in the Wasatch and Uinta Mountains.

Previous research in Rock Canyon and on Mount Timpanogos indicated that bighorn sheep captured in different source areas and released into adjacent locations within the same ecoregion adjusted timing and synchrony of births after four birthing seasons (Whiting *et al.* 2011); therefore, for collared bighorns on the Newfoundland Mountains and on Mount Timpanogos, we used only birthdates of young from females restored to

Table 2. Study areas, dates of release, source populations and demographics of bighorn sheep that were reintroduced to mountain ranges in Utah, USA

Release area	Date	Capture location	Females	Males	Young	Total
Central Basin and Range						
Antelope Island	March 1996	Kamloops, BC, Canada	18	4	4	26
Antelope Island	February 2000	Winnemucca, NV, USA	2	4	0	6
Newfoundland Mountains	January 2001	Hart Mountain, NV, USA	12	3	1	16
Newfoundland Mountains	February 2001	Antelope Island, UT, USA	6	7	2	15
Newfoundland Mountains	February 2003	Antelope Island, UT, USA	13	6	1	20
Stansbury Mountains	Dec. 2005/Jan. 2006	Antelope Island, UT, USA	32	13	12	57
Wasatch and Uinta Mountains						
Mount Timpanogos	January 2000	Rattlesnake Canyon, UT, USA	16	6	3	25
Mount Timpanogos	January 2001	Hinton, Alberta, Canada	8	2	0	10
Mount Timpanogos	February 2002	Sula, MT, USA	6	2	1	9
Rock Canyon	January 2001	Hinton, Alberta, Canada	15	4	3	22

those areas for at least four birthing seasons. Consequently, we did not use birthdates from identifiable females from the 2003 Newfoundland Mountains release during 2005 and 2006 ($n=13$). Also, we did not use one birthdate from an identifiable female from the 2002 Mount Timpanogos release during 2005. Additionally, eight uncollared females from those releases could have been included in our calculation of birthdates of young, because we could not distinguish them from other uncollared females. Data for birthdates in Rock Canyon and on Mount Timpanogos were adapted from Whiting *et al.* (2011).

We relocated collared and uncollared females to record birthdates from 31 March to 5 July from 2005 to 2007. We searched the Central Basin and Range Mountains a mean (\pm s.d.) of every 4 ± 3.0 days, and we searched the Wasatch and Uinta Mountains every 5 ± 3.5 days. We observed several neonates <24-h old, and we estimated birthdates on the basis of behaviour of females before, during and after parturition (Whiting *et al.* 2010b, 2011). We also used first sighting, motor ability, size, and behaviour of neonates to estimate the age of young (Whiting *et al.* 2010b, 2011). To determine birthdates for neonates of uncollared females, we compared their young with neonates of estimated ages of collared females when all females congregated in nursery bands after parturition (Côté and Festa-Bianchet 2001; Whiting *et al.* 2008). We exercised care not to disturb females with young (Gannon and Sikes 2007).

Differential use of elevation by indigenous populations of bighorn sheep is an important factor influencing the timing and synchrony of births across the distribution of this species, especially when comparisons are made among multiple populations (Bunnell 1982; Thompson and Turner 1982). To quantify the use of elevation, we observed groups of collared bighorns using radio-telemetry equipment, binoculars and spotting scopes from January 2005 to December 2007 (Whiting *et al.* 2010b, 2011). Those groups included at least one adult female. We imported those locations onto maps by using ArcGIS (ESRI, Redlands, California, USA; Whiting *et al.* 2010b, 2011). We then overlaid those maps with 10-m resolution digital-elevation models, and each location was ascribed a value for elevation in metres (Whiting *et al.* 2010b, 2011). As

with timing and synchrony of births, we did not use locations of identifiable females when they were alone from the 2003 Newfoundland Mountains release during 2005 and 2006 and from identifiable females from the 2002 Mount Timpanogos release during 2005.

The normalised difference vegetation index (NDVI) is satellite imagery that measures greenness of vegetation, and has been used successfully to link growth of vegetation with animal ecology (Pettoirelli *et al.* 2005, 2011), as well as to compare the onset of plant growth with timing of births in ungulates (Loe *et al.* 2005). We tested for differences in NDVI values between the Central Basin and Range and the Wasatch and Uinta Mountains ecoregions by calculating 95% utilisation distributions for bighorn sightings in each population, using the reference bandwidth in R. We clipped those 95% utilisation distributions by elevation contour lines to exclude features that were not suitable habitat (i.e. the urban interfaces along the Wasatch Front). We used the 250-m, 7-day composite, moderate resolution imaging spectroradiometer (eMODIS-TERRA, <http://pubs.usgs.gov/of/2010/1055/>, verified 18 November 2011) to extract mean weekly values for NDVI in each area from 2001 to 2007. We chose 2001 as the beginning year of those analyses, because it corresponded with when the last populations (Rock Canyon and the Newfoundland Mountains) were established. Thereafter, environmental conditions of release sites could begin to influence life-history characteristics in all populations. We then calculated the yearly initiation of green-up, rate of green-up and timing of peak green-up by ecoregion, using adaptive Savitzky–Golay filtering in TIMESAT 3.02 (Jönsson and Eklundh 2002, 2004).

Data analyses

We estimated birthdates of young, pooled them into sampling intervals (\leq every 5 days, as indicated previously), and calculated corrected means (timing of births) and s.d. values (variance of births) for each population in each year (Johnson *et al.* 2004; Whiting *et al.* 2011). This technique allows robust comparisons of unequal sampling intervals (bin sizes) in determining timing and synchrony of births (Johnson *et al.* 2004). To test for differences between birthdates of populations

occupying the Central Basin and Range Mountains and those on the Wasatch and Uinta Mountains, we averaged birthdates by ecoregion and computed 95% confidence intervals (CIs). We also tested for differences in synchrony of births between those populations by averaging the s.d. values by ecoregion and then computing 95% CIs.

To test for differences in timing of births for bighorn sheep on Antelope Island (source area) compared with the Stansbury Mountains (ecologically similar release site), we calculated corrected means and s.d. values of birthdates for each population in each year using the equations in Johnson *et al.* (2004). We then used those means and s.e. values to construct 95% CIs to test for differences in timing of births between areas for each year (Whiting *et al.* 2008). To determine whether synchrony of births was different between Antelope Island and Stansbury Mountains for each year, we used the corrected s.d. values to calculate coefficients of variation (CVs). We then used Z-tests to examine differences in the CVs for each year (Zar 1999).

We tested for differences in the use of elevation by bighorn sheep in populations that occupied the Central Basin and Range and Wasatch and Uinta Mountains, as well as on Antelope Island (source area) compared with the Stansbury Mountains (ecologically similar release site), using unequal variance *t*-tests (Ruxton 2006). To assess differences in initiation of green-up, rate of green-up and timing of peak green-up, we calculated NDVI values for those variables for each population in each year. We then calculated a mean weekly value (starting at 1 January) for initiation of green-up and timing of peak green-up, as well as a scaled value of NDVI per week for the rate of green-up in areas occupied by populations in the Central Basin and Range and the Wasatch and Uinta Mountains across all years. We compared those mean values between the ecoregions by using 95% CIs.

Results

We recorded birthdates for 178 neonates in the Central Basin and Range Mountains and for 56 neonates on the Wasatch and Uinta Mountains from 2005 to 2007. Across those years, females in populations occupying the Central Basin and Range Mountains gave birth 29 days earlier (mean = 19 April, range = 14–25 April) than did females in populations on the Wasatch and Uinta Mountains (mean = 18 May, range = 9–27 May; Fig. 2). No difference occurred in the synchrony of births (means and CIs) between populations in the Central Basin and Range (mean ± CI, 7 ± 4.3 days) and those on the Wasatch and Uinta Mountains (9 ± 7.6 days).

We observed 718 groups of bighorn sheep that were used to compare the use of elevation between the populations in the Central Basin and Range Mountains and those on the Wasatch and Uinta Mountains. Bighorn sheep that occupied the Central Basin and Range Mountains used elevations (*n* = 337, mean = 1643 m, s.d. = 150.6 m) that were an average of 370 m lower than those used by bighorns on the Wasatch and Uinta Mountains (*n* = 381, mean = 2013 m, s.d. = 280.3 m; *t*' = -22.39, *P* < 0.001). From 2001 to 2007, mean (±95% CIs) initiation of green-up was 4 weeks earlier in the Central Basin and Range (mean = 8 weeks, CI = 1.4 weeks) than on the Wasatch and

Uinta Mountains (mean = 12 weeks, CI = 2.0 weeks). Mean rate of green-up was slower in the Central Basin and Range (mean = 2 NDVI week⁻¹, CI = 0.9 NDVI week⁻¹) than on the Wasatch and Uinta Mountains (mean = 4 NDVI week⁻¹, CI = 0.9 NDVI week⁻¹), and the mean time of peak green-up was 7 weeks earlier in the Central Basin and Range (mean = 22 weeks, CI = 2.4 weeks) than on the Wasatch and Uinta Mountains (mean = 29 weeks, CI = 0.6 weeks).

To compare differences in timing and synchrony of births between bighorn sheep occupying a source area (Antelope Island) and those occupying an ecologically similar release site (the Stansbury Mountains), we recorded birthdates for 67 neonates on Antelope Island and 40 young on the Stansbury Mountains during 2006 and 2007. Timing of births was similar between those two areas in 2006, and females on the Antelope Island gave birth 6 days earlier than those on the Stansbury Mountains in 2007 (Fig. 3); however, no difference existed in timing of births across years between females on Antelope Island and those on the Stansbury Mountains (Fig. 3). In 2006, synchrony of parturition was not significantly different between the Antelope Island females (s.d. = 7.9 days, CV = 7.5%) and the Stansbury Mountain females (s.d. = 6.6 days, CV = 6.4%; Z-test, *Z* = 0.72, *P* = 0.48);

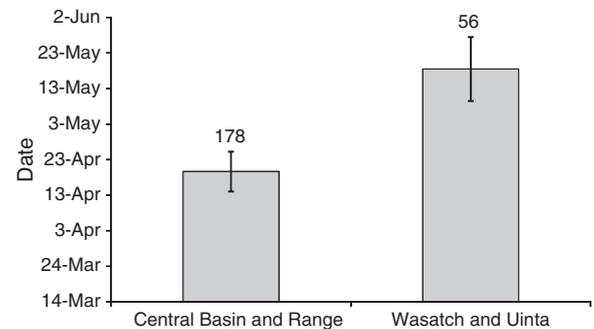


Fig. 2. Mean birthdates (sample size above bars) across years (with 95% CIs) for four populations of bighorn sheep that were reintroduced into adjacent ecoregions in Utah, USA, from 2005 to 2007.

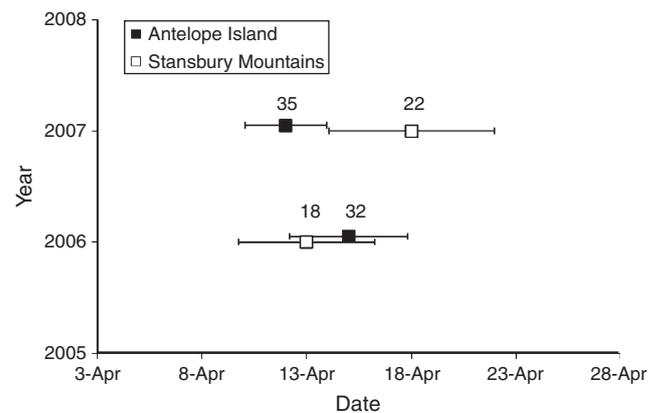


Fig. 3. Mean birthdates, 95% CIs and the number of young born (above the mean) for reintroduced bighorn sheep in two populations separated by 36 km in the Central Basin and Range Ecoregion of northern Utah, USA.

however, in 2007, synchrony of parturition was protracted almost twice as long for females on the Stansbury Mountains (s.d.=9.0 days, CV=8.4%) as for those on Antelope Island (s.d.=5.7 days, CV=5.6%; Z-test, $Z=2.14$, $P=0.04$).

We observed 469 groups of bighorn sheep to test for differences in the use of elevation between groups of females from Antelope Island and those from the Stansbury Mountains. Bighorns on Antelope Island used elevations that were an average of 130 m lower ($n=107$, mean=1669 m, s.d.=103.3 m) than those used by animals on the Stansbury Mountains ($n=362$, mean=1799 m, s.d.=228.6 m; $t'=-8.31$, $P<0.001$).

Discussion

Although only separated by 57 km, female bighorn sheep in two populations occupying the Central Basin and Range Mountains gave birth an average of 29 days earlier than did females in two populations on the Wasatch and Uinta Mountains. Year-round, females in the Central Basin and Range Mountains used elevations that were an average of 370 m lower than those used by bighorns that occupied areas on the Wasatch and Uinta Mountains. Moreover, average initiation of green-up was 4 weeks earlier and peak green-up was ~7 weeks earlier in the Central Basin and Range Mountains. Differential use of elevation by indigenous, female ungulates can influence timing and synchrony of births (Bunnell 1982; Thompson and Turner 1982), even between adjacent populations that occupy different elevations (Bowyer 1991). Also, ungulates occupying areas with early green-up of vegetation, as determined by NDVI values, give birth earlier (Loe *et al.* 2005). The earlier birthdates we documented in bighorn populations in the Central Basin and Range Mountains were most likely produced by females adjusting to earlier green-up of vegetation, or by those animals using lower elevations that had differences in snow accumulation (Loe *et al.* 2005), soil moisture, plant communities (Douglas 2001) and phenological development of plants (Festa-Bianchet 1986; Berger 1991). Our results indicated that populations of bighorn sheep reintroduced into adjacent ecoregions adjusted timing of births to differences in the environment and green-up of vegetation in restoration areas. We hypothesise that females adjusted the length of gestation, which has also been documented in other ungulates (Rachlow and Bowyer 1991; Berger 1992; Schwartz and Hundertmark 1993).

Timing of births was similar across years for female bighorn sheep on the Stansbury Mountains (ecologically similar release area) compared with those on Antelope Island (source population). Further, even though bighorns on the Stansbury Mountains could have used areas of high elevation, they used elevations that were only 130 m higher than areas used by bighorns on Antelope Island. These mountain ranges are separated by 36 km and are located in the Central Basin and Range Ecoregion. The idea of ecological similarity has been used in plant restorations (Lawrence and Kaye 2011; Noël *et al.* 2011). This idea has been adopted by some wildlife biologists that have considered birthing times of reintroduced bighorn sheep and have tried to match environments of release sites with those of capture locations (Stockton 2005a, 2005b); however, quantitative evidence of this phenomenon is lacking. Our

results provided evidence that timing and synchrony of births for reintroduced bighorn sheep in an ecologically similar release site were similar to those in their source area, and that ecological similarity needs to be considered when restoring bighorn populations.

Most bighorn sheep on Antelope Island came from areas near Kamloops, British Columbia, Canada (those areas are separated by >1245 km). Females from that source area usually give birth in May and early June (Demarchi and Mitchell 1973; Demarchi *et al.* 2000). Bighorn sheep on Antelope Island gave birth ~1 month earlier than did females from their source areas in British Columbia. Additionally, other populations of bighorn sheep captured in British Columbia and released into areas in the south-western United States adjusted birthing to mid-April (Demarchi *et al.* 2000), similar to what we observed. These results support previous work, indicating that bighorn sheep adjust timing and synchrony of births to the environment of their release sites; however, adjustment of these life-history events occurred after 4 years (Whiting *et al.* 2011). Therefore, this time lag in adjustment of life-history characteristics needs to be considered when restoring populations of bighorn sheep, especially when survival or reproductive rates may be low as animals become accustomed to conditions of their release site (Armstrong and Seddon 2008; Whiting *et al.* 2011).

Reintroductions of bighorn sheep are the primary way in which biologists and conservationists restore populations of these ungulates (Bleich *et al.* 1990; Krausman 2000). Reintroductions of bighorns, however, oftentimes only consist of ~20 animals (Douglas and Leslie 1999), and the average number of animals initially released into our study areas was 29. Reintroductions with more animals (≥ 41 bighorns) had greater success than those with fewer animals (Singer *et al.* 2000). When releasing bighorns into habitats that are ecologically dissimilar from their source areas, the effects of slow adjustment of timing and synchrony of births of young – and the subsequent decrease in survival and reproductive potential of late-born young to their first winter – could possibly be minimised if more bighorns were initially released.

Reintroductions are likely to proceed at an increasing rate, especially with habitat loss and fragmentation further threatening bighorn populations (Hein 1997; Seddon *et al.* 2007). Populations of bighorn sheep have declined significantly, and these ungulates face a precarious future (Buechner 1960; Geist 1971). These animals are some of the rarest ungulates in North America, with some populations listed as endangered (Krausman 2000; Schroeder *et al.* 2010). Much can be learned to improve reintroduction techniques and enhance successful restoration of bighorn populations (Shannon *et al.* 2008; Whiting *et al.* 2011). Such information is a pressing conservation issue for these ungulates. Our results indicate that adjustment of timing and synchrony of births needs to be considered in reintroductions, especially when releasing bighorns into different ecoregions. We thus support the management practice of capturing and releasing individuals from ecologically similar locations, which may reduce the negative effects of young being born late, such as decreased survival to their first winter and yearling age, as well as reduced future reproductive potential (Clutton-Brock *et al.* 1987; Festa-Bianchet *et al.* 2000; Keech *et al.* 2000).

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References

- Armstrong, D. P., and Seddon, P. J. (2008). Directions in reintroduction biology. *Trends in Ecology & Evolution* **23**, 20–25. doi:10.1016/j.tree.2007.10.003
- Berger, J. (1991). Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. *Animal Behaviour* **41**, 61–77. doi:10.1016/S0003-3472(05)80503-2
- Berger, J. (1992). Facilitation of reproductive synchrony by gestation adjustment in gregarious mammals: a new hypothesis. *Ecology* **73**, 323–329. doi:10.2307/1938743
- Bleich, V. C., Wehausen, J. D., and Holl, S. A. (1990). Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. *Conservation Biology* **4**, 383–390. doi:10.1111/j.1523-1739.1990.tb00312.x
- Bowyer, R. T. (1991). Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* **72**, 138–145. doi:10.2307/1381988
- Buechner, H. K. (1960). The bighorn sheep in the United States, its past, present, and future. *Wildlife Monographs* **4**, 1–174.
- Bunnell, F. L. (1980). Factors controlling lambing period of Dall's sheep. *Canadian Journal of Zoology* **58**, 1027–1031. doi:10.1139/z80-144
- Bunnell, F. L. (1982). The lambing period of mountain sheep: synthesis, hypotheses, and tests. *Canadian Journal of Zoology* **60**, 1–14. doi:10.1139/z82-001
- Clutton-Brock, T. H., Major, M., Albon, S. D., and Guinness, F. E. (1987). Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. *Journal of Animal Ecology* **56**, 53–67. doi:10.2307/4799
- Côté, S. D., and Festa-Bianchet, M. (2001). Birthdate, mass and survival in mountain goat kids: effects of maternal characteristics and forage quality. *Oecologia* **127**, 230–238. doi:10.1007/s004420000584
- Demarchi, D. A., and Mitchell, H. B. (1973). The Chilcotin River bighorn population. *Canadian Field-Naturalist* **87**, 433–454.
- Demarchi, R. A., Hartwig, C. L., and Demarchi, D. A. (2000). 'Status of California Bighorn Sheep in British Columbia.' (BC Ministry of Environment, Lands, and Parks, Wildlife Branch: Victoria, BC, Canada.)
- Douglas, C. L. (2001). Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. *Wildlife Society Bulletin* **29**, 297–305.
- Douglas, C. L., and Leslie, D. M. (1999). Management of bighorn sheep. In 'Mountain Sheep of North America'. (Eds R. Valdez and P. R. Krausman.) pp. 238–262. (The University of Arizona Press: Tucson, AZ.)
- Festa-Bianchet, M. (1986). Seasonal dispersion of overlapping mountain sheep ewe groups. *The Journal of Wildlife Management* **50**, 325–330. doi:10.2307/3801922
- Festa-Bianchet, M. (1988). Birthdate and survival in bighorn lambs (*Ovis canadensis*). *Journal of Zoology* **214**, 653–661. doi:10.1111/j.1469-7998.1988.tb03764.x
- Festa-Bianchet, M., Jorgenson, J. T., and Réale, D. (2000). Early development, adult mass, and reproductive success in bighorn sheep. *Behavioral Ecology* **11**, 633–639. doi:10.1093/beheco/11.6.633
- Gannon, W. L., and Sikes, R. S. (2007). Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* **88**, 809–823. doi:10.1644/06-MAMM-F-185R.1
- Geist, V. (1971). 'Mountain Sheep: a Study in Behavior and Evolution.' (The University of Chicago Press: Chicago, IL.)
- Griffith, B., Scott, J. M., Carpenter, J. W., and Reed, C. (1989). Translocation as a species conservation tool: status and strategy. *Science* **245**, 477–480. doi:10.1126/science.245.4917.477
- Guinness, F. E., Clutton-Brock, T. H., and Albon, S. D. (1978). Factors affecting calf mortality in red deer (*Cervus elaphus*). *Journal of Animal Ecology* **47**, 817–832. doi:10.2307/3673
- Hass, C. C. (1997). Seasonality of births in bighorn sheep. *Journal of Mammalogy* **78**, 1251–1260. doi:10.2307/1383068
- Hein, E. W. (1997). Improving translocation programs. *Conservation Biology* **11**, 1270–1271.
- Ims, R. A. (1990). The ecology and evolution of reproductive synchrony. *Trends in Ecology & Evolution* **5**, 135–140. doi:10.1016/0169-5347(90)90218-3
- Johnson, D. S., Barry, R. P., and Bowyer, R. T. (2004). Estimating timing of life-history events with coarse data. *Journal of Mammalogy* **85**, 932–939. doi:10.1644/BFW-009
- Jönsson, P., and Eklundh, L. (2002). Seasonality extraction by function fitting to time-series of satellite sensor data. *IEEE Transactions on Geoscience and Remote Sensing* **40**, 1824–1832. doi:10.1109/TGRS.2002.802519
- Jönsson, P., and Eklundh, L. (2004). TIMESAT – a program for analyzing time-series of satellite sensor data. *Computers & Geosciences* **30**, 833–845. doi:10.1016/j.cageo.2004.05.006
- Keech, M. A., Bowyer, R. T., Ver Hoef, J. M., Boertje, R. D., Dale, B. W., and Stephenson, T. R. (2000). Life-history consequences of maternal condition in Alaskan moose. *The Journal of Wildlife Management* **64**, 450–462. doi:10.2307/3803243
- Krausman, P. R. (2000). An introduction to the restoration of bighorn sheep. *Restoration Ecology* **8**, 3–5. doi:10.1046/j.1526-100x.2000.80060.x
- Krausman, P. R., and Bowyer, R. T. (2003). Mountain sheep (*Ovis canadensis* and *O. dalli*). In 'Wild Mammals of North America: Biology, Management, and Conservation'. (Eds G. A. Feldhamer, B. C. Thompson and J. A. Chapman.) pp. 1095–1115. (The John Hopkins University Press: Baltimore, MD.)
- Lawrence, B. A., and Kaye, T. N. (2011). Reintroduction of *Castilleja levisecta*: effects of ecological similarity, source population genetics, and habitat quality. *Restoration Ecology* **19**, 166–176. doi:10.1111/j.1526-100X.2009.00549.x
- Lenarz, M. S. (1979). Social structure and reproductive strategy in desert bighorn sheep (*Ovis canadensis mexicana*). *Journal of Mammalogy* **60**, 671–678. doi:10.2307/1380184
- Loe, L. E., Bonenfant, C., Mysterud, A., Gaillard, J.-M., Langvatn, R., Klein, F., Calenge, C., Ergon, T., Pettorelli, N., and Stenseth, N. C. (2005). Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *Journal of Animal Ecology* **74**, 579–588. doi:10.1111/j.1365-2656.2005.00987.x
- Marshall, F. H. A., and Cambridge, F. R. S. (1937). On the change over in the oestrous cycle in animals after transference across the equator, with further observations on the incidence of the breeding seasons and the factors controlling sexual periodicity. *Proceedings of the Royal Society of London. Series B, Biological Sciences* **122**, 413–428. doi:10.1098/rspb.1937.0034
- Noël, F., Prati, D., van Kleunen, M., Gygas, A., Moser, D., and Fischer, M. (2011). Establishment success of 25 rare wetland species introduced into restored habitats is best predicted by ecological distance to source habitats. *Biological Conservation* **144**, 602–609. doi:10.1016/j.biocon.2010.11.001
- Olson, D. D., Shannon, J. M., Whiting, J. C., and Flinders, J. T. (2008). History, status, and population structure of California bighorn sheep in Utah. *Proceedings of the Northern Wild Sheep and Goat Council* **16**, 161–177.

- Pettorelli, N., Vik, J. O., Mysterud, A., Gaillard, J. M., Tucker, C. J., and Stenseth, N. C. (2005). Using the satellite-derived NDVI to assess ecological responses to environmental change. *Trends in Ecology & Evolution* **20**, 503–510. doi:10.1016/j.tree.2005.05.011
- Pettorelli, N., Ryan, S., Mueller, T., Bunnefeld, N., Jedrzejewska, B., Lima, M., and Kausrud, K. (2011). The normalized difference vegetation index (NDVI): unforeseen successes in animal ecology. *Climate Research* **46**, 15–27. doi:10.3354/cr00936
- Rachlow, J. L., and Bowyer, R. T. (1991). Interannual variation in timing and synchrony of parturition in Dall's sheep. *Journal of Mammalogy* **72**, 487–492. doi:10.2307/1382131
- Reimers, E., Klein, D. R., and Sørungård, R. (1983). Calving time, growth rate, and body size of Norwegian reindeer on different ranges. *Arctic and Alpine Research* **15**, 107–118. doi:10.2307/1550986
- Rubin, E. S., Boyce, W. M., and Bleich, V. C. (2000). Reproductive strategies of desert bighorn sheep. *Journal of Mammalogy* **81**, 769–786. doi:10.1644/1545-1542(2000)081<0769:RSODBS>2.3.CO;2
- Rutberg, A. T. (1987). Adaptive hypotheses of birth synchrony in ruminants: an interspecific test. *American Naturalist* **130**, 692–710. doi:10.1086/284739
- Ruxton, G. D. (2006). The unequal variance *t*-test is an underused alternative to Student's *t*-test and the Mann–Whitney *U* test. *Behavioral Ecology* **17**, 688–690. doi:10.1093/beheco/ark016
- Sadleir, R. M. F. S. (1969). The role of nutrition in the reproduction of wild mammals. *Journal of Reproduction and Fertility. Supplement* **6**, 39–48.
- Schroeder, C. A., Bowyer, R. T., Bleich, V. C., and Stephenson, T. R. (2010). Sexual segregation in Sierra Nevada bighorn sheep, *Ovis canadensis sierrae*: ramifications for conservation. *Arctic, Antarctic, and Alpine Research* **42**, 476–489. doi:10.1657/1938-4246-42.4.476
- Schwartz, C. C., and Hundertmark, K. J. (1993). Reproductive characteristics of Alaskan moose. *The Journal of Wildlife Management* **57**, 454–468. doi:10.2307/3809270
- Seddon, P. J., Armstrong, D. P., and Maloney, R. F. (2007). Developing the science of reintroduction biology. *Conservation Biology* **21**, 303–312. doi:10.1111/j.1523-1739.2006.00627.x
- Shannon, J. M., Olson, D. D., Whiting, J. C., Flinders, J. T., and Smith, T. S. (2008). Status, distribution, and history of Rocky Mountain bighorn sheep in Utah. *Proceedings of the Northern Wild Sheep and Goat Council* **16**, 178–195.
- Singer, F. J., Papouchis, C. M., and Symonds, K. K. (2000). Translocations as a tool for restoring populations of bighorn sheep. *Restoration Ecology* **8**, 6–13. doi:10.1046/j.1526-100x.2000.80061.x
- Smith, T. S., Flinders, J. T., and Olsen, D. W. (1988). Status and distribution of Rocky Mountain bighorn sheep in Utah. *Biennial Symposium of the Northern Wild Goat and Sheep Council* **6**, 5–12.
- Stockton, T. (2005a). Bringing them back *Wyoming Wildlife*. Wyoming Game and Fish Department, Cheyenne, WY, pp. 24–31.
- Stockton, T. (2005b). A look to the future *Wyoming Wildlife*. Wyoming Game and Fish Department, Cheyenne, WY, pp. 32–37.
- Thompson, R. W., and Turner, J. C. (1982). Temporal geographic variation in the lambing season of bighorn sheep. *Canadian Journal of Zoology* **60**, 1781–1793. doi:10.1139/z82-231
- Wehausen, J. D., and Ramey, R. R. (2000). Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis*. *Journal of Mammalogy* **81**, 145–161. doi:10.1644/1545-1542(2000)081<0145:CMAERI>2.0.CO;2
- Whiting, J. C., Bowyer, R. T., and Flinders, J. T. (2008). Young bighorn (*Ovis canadensis*) males: can they successfully woo females? *Ethology* **114**, 32–41. doi:10.1111/j.1439-0310.2007.01442.x
- Whiting, J. C., Bowyer, R. T., and Flinders, J. T. (2009a). Annual use of water sources by reintroduced Rocky Mountain bighorn sheep *Ovis canadensis canadensis*: effects of season and drought. *Acta Theriologica* **54**, 127–136. doi:10.1007/BF03193168
- Whiting, J. C., Bowyer, R. T., and Flinders, J. T. (2009b). Diel use of water by reintroduced bighorn sheep. *Western North American Naturalist* **69**, 407–412. doi:10.3398/064.069.0318
- Whiting, J. C., Bowyer, R. T., Flinders, J. T., Bleich, V. C., and Kie, J. G. (2010a). Sexual segregation and use of water by bighorn sheep: implications for conservation. *Animal Conservation* **13**, 541–548. doi:10.1111/j.1469-1795.2010.00370.x
- Whiting, J. C., Stewart, K. M., Bowyer, R. T., and Flinders, J. T. (2010b). Reintroduced bighorn sheep: do females adjust maternal care to compensate for late-born young? *European Journal of Wildlife Research* **56**, 349–357. doi:10.1007/s10344-009-0323-y
- Whiting, J. C., Bowyer, R. T., Flinders, J. T., and Eggett, D. L. (2011). Reintroduced bighorn sheep: fitness consequences of adjusting parturition to local environments. *Journal of Mammalogy* **92**, 213–220. doi:10.1644/10-MAMM-A-145.1
- Zar, J. H. (1999). 'Biostatistical Analysis.' (Prentice-Hall: Upper Saddle River, NJ)