



Research Article

Desert Bighorn Sheep Lambing Habitat: Parturition, Nursery, and Predation Sites

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ABSTRACT Fitness of female ungulates is determined by neonate survival and lifetime reproductive success. Therefore, adult female ungulates should adopt behaviors and habitat selection patterns that enhance survival of neonates during parturition and lactation. Parturition site location may play an important role in neonatal mortality of desert bighorn sheep (*Ovis canadensis mexicana*) when lambs are especially vulnerable to predation, but parturition sites are rarely documented for this species. Our objectives were to assess environmental characteristics at desert bighorn parturition, lamb nursery, and predation sites and to assess differences in habitat characteristics between parturition sites and nursery group sites, and predation sites and nursery group sites. We used vaginal implant transmitters (VITs) to identify parturition sites and capture neonates. We then compared elevation, slope, terrain ruggedness, and visibility at parturition, nursery, and lamb predation sites with paired random sites and compared characteristics of parturition sites and lamb predation sites to those of nursery sites. When compared to random sites, odds of a site being a parturition site were highest at intermediate slopes and decreased with increasing female visibility. Odds of a site being a predation site increased with decreasing visibility. When compared to nursery group sites, odds of a site being a parturition site had a quadratic relationship with elevation and slope, with odds being highest at intermediate elevations and intermediate slopes. When we compared predation sites to nursery sites, odds of a site being a predation were highest at low elevation areas with high visibility and high elevation areas with low visibility likely because of differences in hunting strategies of coyote (*Canis latrans*) and puma (*Puma concolor*). Parturition sites were lower in elevation and slope than nursery sites. Understanding selection of parturition sites by adult females and how habitat characteristics at these sites differ from those at predation and nursery sites can provide insight into strategies employed by female desert bighorn sheep and other species during and after parturition to promote neonate survival. © 2016 The Wildlife Society.

KEY WORDS birth site, desert bighorn sheep, lamb survival, *Ovis canadensis mexicana*, parturition, predation, vaginal-implant transmitter.

Differences in age-specific mortality rates are strongly linked with population dynamics of large ungulates (Gaillard et al. 2000). Change in survival of reproductive age females has a large potential to influence population growth; however, because adult female survival typically varies little from year to year, changes in population growth are often related to juvenile survival rates (Gaillard et al. 1998, 2000; Owen-Smith and Mason 2005). Juvenile ungulates are most susceptible to mortality shortly after parturition, with

predation often being the leading cause of mortality (Linnell et al. 1995, Gaillard et al. 2000). Given the association between lifetime reproductive success and fitness, female ungulates should employ behaviors that improve offspring survival during parturition and lactation.

Natural selection should favor adult females that display behaviors and habitat selection patterns that enhance neonate survival (Festa-Bianchet 1988, Bleich et al. 1997). For example, females should select habitat with conditions that reduce predation risk for their offspring even if it comes at the expense of better foraging opportunities for themselves (Festa-Bianchet 1988, Berger 1991, Bleich et al. 1997, Côté and Hamel 2007, Ciuti et al. 2009). Studies on post-parturition habitat selection of a variety of ungulate species are generally consistent in their results; during lactation when offspring are vulnerable to predation, habitat selection

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of adult females is associated with hiding cover for neonates and other habitat characteristics (e.g., steep, rocky terrain) that facilitate predator avoidance (Bleich et al. 1997, Ciuti et al. 2006, Pitman et al. 2014, Smith et al. 2015). Females with young at heel select safer areas than barren females or those that lost their young (Kohlmann et al. 1996; Mooring et al. 2003; Grignolio et al. 2007; Ciuti et al. 2006, 2009). This pattern of habitat selection during the post-parturition lactation period is evident even in areas with reduced predation risk due to low predator abundance (Mooring et al. 2003, Grignolio et al. 2007).

Parturient females isolate themselves from the herd immediately prior to giving birth and remain isolated a few days to a few weeks; the duration of isolation varies across species. This isolation period serves to establish the mother-young bond and reduce predation risk on neonates (Hansen and Deming 1980, Ciuti et al. 2009). Although used for a much shorter period of time than post-parturition habitat, the characteristics at the parturition sites also play an important role in reducing neonatal mortality (Bergerud and Page 1987, Canon and Bryant 1997, Bowyer et al. 1999, Wiseman et al. 2006, Rearden et al. 2011). Parturition site characteristics have been investigated for a number of ungulate species (e.g., elk [*Cervus elaphus*], Rearden et al. 2011; mule deer [*Odocoileus hemionus*], Speten 2014; pronghorn [*Antilocapra americana*], Alldredge et al. 1991); however, data on habitat characteristics at parturition sites for some species have not been investigated, particularly for some mountain ungulates and species that occupy remote, difficult to access areas.

Desert bighorn sheep (*Ovis canadensis mexicana*) are one such species. Although bighorn lambs fall under the follower classification (Lent 1974, Carl and Robbins 1988), for the first few days of life, lambs tend to employ a hider strategy near the parturition site because of their inability to keep up with their mothers (Karsch 2014). Previous studies report that female bighorn select lambing areas (i.e., areas where females give birth and raise lambs their first few months of life) with high elevation, steeper slopes with rocky outcroppings, and good visibility (Geist 1971, Hansen 1980a, DeForge and Scott 1982, Shackleton et al. 1999). However, previous reports of lambing areas were largely based on the presence of lambs and not on observations of birth (Bangs et al. 2005, Smith et al. 2015); thus, these sites were likely nursery sites but it is uncertain if these areas are also used for parturition. A recent study of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in the Black Hills of South Dakota reported that >80% of documented parturition events occurred outside of previously identified lambing areas (Smith et al. 2015).

Whether or not areas traditionally defined as lambing habitat for desert bighorn sheep are also used for parturition is unknown. In comparison to other ungulates, the rugged nature their habitat and remote location of most desert bighorn populations has limited research on parturition sites, behavior, survival, and causes of mortality for neonates. It is unknown if desert bighorn sheep use discrete parturition areas that are used by multiple females or if there is fidelity to

such sites across years (Etchberger and Krausman 1999, Krausman and Shackleton 2000, Goldstein 2001), and rarely are lamb carcasses found to provide information on mortality events. The most common causes of desert bighorn lamb mortality include predation, disease, and falls (Etchberger and Krausman 1999, Parsons 2007); however, the timing of or the environmental characteristics associated with mortality events are largely undocumented because of difficulty locating carcasses of uncollared animals (Krausman and Shackleton 2000, Goldstein 2001) and a lack of information derived from monitoring radio-collared lambs.

Our objectives were to assess environmental characteristics at desert bighorn parturition, lamb nursery, and predation sites and to assess differences in habitat characteristics between parturition sites and nursery group sites, and predation sites and nursery group sites. We predicted that female desert bighorn would select parturition and nursery sites at higher elevations, on steeper slopes, and in more rugged terrain that afforded greater visibility. Accordingly, we predicted that we would find little difference in habitat characteristics between parturition and nursery group sites. We predicted lamb predation sites would be at lower elevations, on less steep slopes, and in less rugged terrain with lower visibility than nursery group sites.

STUDY AREA

The Peloncillo Mountains are located in Hidalgo County, southwestern New Mexico, and extend approximately 120 km from the United States-Mexico border into Arizona. Our study area encompassed 83 km² of mountainous terrain just west of Animas, New Mexico (Fig. 1); elevations range from 1,265 m to 1,698 m. The majority of the range was managed by the Bureau of Land Management, interspersed with some state trust and private lands. Vegetation was composed of semi-desert grassland and Chihuahuan desert scrub (Dick-Peddie 1993, Brown 1994). Predators included pumas (*Puma concolor*), bobcats (*Lynx rufus*), coyotes (*Canis latrans*), gray fox (*Urocyon cinereoargenteus*), and golden eagles (*Aquila chrysaetos*). Common ungulates included collared peccary (*Pecari tajacu*), mule deer, and domestic cattle.

Climate in the Peloncillo Mountains was characterized by a monsoon precipitation cycle with 54% of rain occurring from July–September (Western Regional Climate Center [WRCC] 2014). Long-term (1960–2013) mean annual precipitation was 28.2 cm (SD = 8.94 cm; National Oceanic and Atmospheric Administration 2014; Animas, NM ~10 km east of the study area). Maximum temperatures occurred June–August with an average high temperature of 34.2°C and a low of 16.8°C. Minimum monthly temperatures occurred December–February with an average high of 15.2°C and a low of –1.6°C (WRCC 2014, 1975–2013).

METHODS

In November 2011, we captured 20 pregnant adult female bighorn using a net gun fired from a helicopter (Krausman et al. 1985); we captured 11 in the Fra Cristobal Mountains and 9 from the Red Rock Wildlife Management Area, New

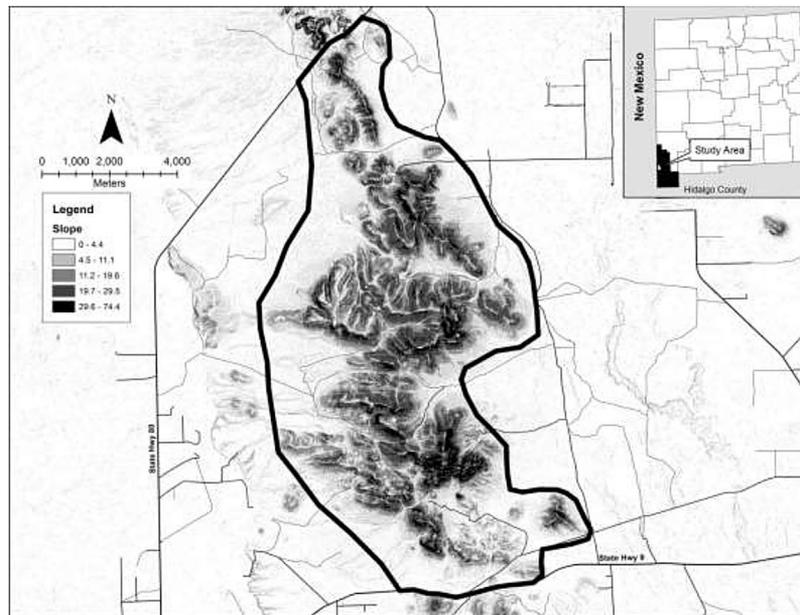


Figure 1. The central Peloncillo Mountains, New Mexico, USA.

Mexico, USA. In December 2012, we captured 19 pregnant females in the Peloncillo Mountains in the same manner, 14 of which were study animals originally captured in 2011. We used a portable ultrasound (Sonosite Vet 180 Plus, Ocean-side, CA, USA; Duquette et al. 2012) to determine pregnancy status and fit pregnant animals with uniquely colored, very high frequency (VHF) radiocollars equipped with a 6-hour mortality sensor (2011, model 2520B, Advanced Telemetry Systems, Isanti, MN, USA; 2012, model V5C 181C, Sirtrack, North Liberty, IA, USA), a unique ear tag, and a vaginal implant transmitter (VIT; model PETTMPF2, Advanced Telemetry Systems). The VITs were designed to be expelled at parturition and contained a temperature-sensitive switch that caused an increase in pulse rate when temperature fell below 30°C when the VIT was expelled during parturition. Handling time for each animal was ≤ 15 minutes. We transported bighorn captured in 2011 in a partially enclosed trailer to the Peloncillo Mountains for release in an area occupied by resident desert bighorn sheep. In 2012, we captured bighorn in the Peloncillo Mountains, flew them to a handling location within the study area, and released them from the handling location back onto the mountain.

Beginning in December of each year, we monitored VITs 1–2 times/day. Upon hearing the increased pulse rate associated with an expelled VIT, we immediately attempted to visually locate the adult female through a spotting scope from a distance of >500 m to observe her behavior and search for a lamb in her vicinity. Once located, 1 person monitored the female and lamb through the scope, while a 2-person team approached to capture the lamb (Smith et al. 2014). Upon capture, we manually restrained, blindfolded, and fit the lamb with an expandable VHF collar equipped with a 6-hour mortality sensor (Model M4210, Advanced Telemetry Systems). We inserted a numbered ear tag,

determined sex, and recorded morphometric measurements. Handling time was ≤ 15 minutes, and we released lambs at site of capture. After release, we continued monitoring the lamb via spotting scope to determine if it reunited with its mother, and recorded elapsed time from release to reunion (Karsch 2014). All animal capture and handling procedures were approved by New Mexico State University's Institutional Animal Care and Use Committee (IACUC protocol #2011-026).

We monitored lambs daily from capture until 16 weeks of age, every 2–4 days until 6 months of age, and weekly thereafter until they were approximately 1 year old or the collar dropped off. If we detected a mortality signal, we located the animal to examine the carcass and vicinity within 100 m to determine cause of death. We recorded the mortality site description and coordinates, appearance of the carcass, and evidence of prior injuries or disease. If the carcass was relatively fresh and cause of death was not apparent, we performed a necropsy and sent tissue samples to the New Mexico Veterinary Diagnostic Services lab for further analysis.

Characteristics indicative of puma kills included cache sites with vegetation, dirt and or rocks covering the carcass, presence of puma tracks, scat, and canine puncture spacing 3.8–5.7 cm on neck, throat or head, uneaten rumen, or rumen removed from the carcass (Halbritter et al. 2008). Coyote and gray fox kills were differentiated from puma kills, and from each other, based on canine puncture spacing (2.9–3.5 cm for coyotes, and 1.27–2.54 cm for gray fox), and tracks at the site (Bowns 1995).

We estimated visual obstruction and determined slope, elevation, and ruggedness at parturition, nursery, lamb predation locations, and at paired random sites. We selected 1 paired random site for each used site by selecting a random distance 50–400 m from the used site and along a randomly

selected compass bearing. We set the minimum distance to prevent the random site from being too close to the used site and set the maximum distance at 400 m to prevent the random site from being located outside of primary habitat for desert bighorn (e.g., in the flats surrounding the mountains). We used VITs to locate parturition sites, which we identified by the presence of birthing fluids and blood in conjunction with freshly exposed soil. We defined a nursery site by the presence of at least 1 lamb >1 week old with ≥ 1 adult female (Karsch 2014). We located nursery sites through observations of collared lambs and adult females, and uncollared lambs and females through regular surveys of nursery areas and incidental sightings. Groups were no longer defined as nursery groups when adult males were present, which began to occur in July prior to the rut, when lambs were between 4 and 7 months of age. However, we located the last nursery sites in early June. In an effort to minimize disturbance to sheep, we did not collect site-characteristic data until sheep moved from the area. If we observed sheep using the same nursery site on >1 occasion, we surveyed that nursery site only once to minimize repeated sampling of the same location and to increase the number of unique nursery locations sampled. The center point for the survey of nursery sites was located at approximately the most central location of the group when they were first sighted.

We approximated an adult female bighorn's visibility of potential predators by recording visibility at each site using a 1.5 m Robel pole (Robel et al. 1970). We placed the Robel pole 15 m from the site in each cardinal direction and viewed it at a height of 88 cm to simulate adult female bighorn eye height (Hansen 1980b). We evaluated slope, elevation, and terrain ruggedness with a United States Geological Survey digital elevation model with 10×10 -m resolution. We calculated vector ruggedness (i.e., topographically uneven, broken, or rocky and steep terrain) using a 5×5 cell neighborhood in ArcGIS 10.0 (ESRI, Redlands, CA, USA) following Sappington et al. (2005), which results in a dimensionless ruggedness index that ranges from 0 (flat) to 1 (most rugged); because of the widely different scales of measurement in our predictor variables, we rescaled ruggedness values by multiplying by 1,000. We calculated slope and elevation in ArcGIS 10.0. Thus we considered our habitat selection analysis for parturition and nursery sites to be at the mesohabitat scale (Mezquida 2004, Moura et al. 2005).

Data Analysis

We used conditional logistic regression for matched-pairs data to compare used sites to paired random sites, and binary logistic regression to compare parturition and predation sites to nursery sites. For conditional logistic regression, we coded the response variable as actual site or random site with actual sites and paired random sites treated as used and available resource units, respectively. For binary logistic regression, the response variable was coded as parturition or predation site, and nursery site. We were specifically interested in determining if there were differences between nursery and parturition sites and comparing characteristics of predation

sites to nursery sites. However, we did not compare parturition and predation sites because we had no a priori reason for this comparison and all documented lamb mortalities occurred after they had departed the parturition sites for the nursery areas; thus, parturition site characteristics were unrelated to lamb mortalities. For all analyses we pooled data across years. In addition, the individual females that were captured and fitted with a VIT in both years of the study were treated as independent samples in our analyses.

Our initial set of explanatory variables included visibility averaged across the 4 cardinal directions, elevation, slope, and ruggedness. We conducted a pairwise correlation analysis to assess the potential for multicollinearity among explanatory variables. Elevation and slope ($r = 0.713$), and elevation and visibility ($r = 0.662$) were correlated in the comparison of predation sites to random sites but were not correlated in any other analyses. Therefore, we did not use individual models containing elevation and visibility in the predation site analysis. However, because these variables were not correlated in other analyses, we retained them individually, or with other covariates in the model set. We developed 26 a priori models using ≤ 3 variables per individual model (Table 1). We selected variables based on biological importance as suggested in previous habitat selection studies of parturient female ungulates (Bergerud et al. 1984, Rachlow and Bowyer 1998, Bowyer et al. 1999,

Table 1. Model structure of 26 a priori models relating to the probability of predicting parturition, nursery, and predation sites for desert bighorn lambs relative to environmental characteristics in the Peloncillo Mountains, New Mexico, USA in the 2012 and 2013 lambing seasons.

Model	Model structure ^a
1	ELEV
2	SLOPE
3	RUGGED
4	VIS
5	ELEV + SLOPE ^b
6	ELEV + RUGGED
7	ELEV + VIS ^b
8	SLOPE + RUGGED
9	SLOPE + VIS
10	RUGGED + VIS
11	ELEV + SLOPE + (ELEV \times SLOPE) ^b
12	ELEV + RUGGED + (ELEV \times RUGGED)
13	ELEV + VIS + (ELEV \times VIS) ^b
14	SLOPE + RUGGED + (SLOPE \times RUGGED)
15	SLOPE + VIS + (SLOPE \times VIS)
16	RUGGED + VIS \times (RUGGED + VIS)
17	ELEV ² + ELEV
18	SLOPE ² + SLOPE
19	RUGG ² + RUGG
20	VIS ² + VIS
21	ELEV + ELEV ² + SLOPE + SLOPE ²
22	ELEV + ELEV ² + RUGG + RUGG ²
23	ELEV + ELEV ² + VIS + VIS ²
24	SLOPE + SLOPE ² + RUGG + RUGG ²
25	SLOPE + SLOPE ² + VIS + VIS ²
26	RUGG + RUGG ² + VIS + VIS ²

^a ELEV, elevation; SLOPE, slope; RUGG, ruggedness; VIS, adult female visibility.

^b Models not included in the analysis of predation and random sites because of correlation between predictor variables.

Krausman et al. 1999, Bangs et al. 2005) and observations made during previous work with desert bighorn sheep. We used an information-theoretic approach to assess model support using Akaike's Information Criterion corrected for small sample sizes (AIC_c ; Burnham and Anderson 2002, Johnson and Omland 2004). We considered models with ΔAIC_c values ≤ 2.0 to have strong support, and values between 2 and 7 to have some support. We used model weight to further examine explanatory power of each model. Only models with an AIC_c weight ≥ 0.05 are presented in the results. We calculated model-averaged parameter estimates ($\pm SE$) and 90% confidence intervals for variables in competing models using multi-model averaging (Burnham and Anderson 2002) across all a priori models. We calculated odds ratios by exponentiation of the model-averaged parameter estimates and 90% confidence limits. We used SPSS version 17 (SPSS Inc., Chicago, Illinois, USA) for all statistical analyses

For models with an interaction term and a $\Delta AIC_c \leq 2$ or a weight ≥ 0.10 , we examined interaction effects graphically. We calculated 25th, 50th, 75th, and 95th percentiles of one of the predictor variables in the interaction term and used these values in the logistic regression equation to model the change in the odds in relation to the second predictor variable in the interaction at each percentile of the first predictor variable. For conditional logistic regression, we analyzed interactions by subtracting the 25th, 50th, 75th, and 95th percentile values of the random site from the actual site; thus, we plotted change in probability in relation to the difference in value between the covariates at used and random sites.

Post hoc, we examined the characteristics of female parturition sites for animals that were fitted with VITs both years of the study using a paired t -test to examine if there was a difference in elevation, slope, ruggedness, or visibility at parturition sites used each year. In addition, we compared characteristics of parturition sites of females native to the Peloncillo Mountains to those translocated during our study using a 2-sample t -test. Because the majority of lamb mortalities resulted from 2 predator species with different life-history characteristics, we also used a 2-sample t -test to explore differences in elevation, slope, ruggedness, and visibility at lamb predation sites classified by predator species.

RESULTS

We captured and fitted 26 neonates with radio-collars (12 in 2012, and 14 in 2013), and located 33 parturition, 26 unique nursery, and 12 predation sites. Seven lambs from females fitted with VITs were not captured, but we were able to conduct surveys at their parturition sites. All neonates were ≤ 2 days old at time of capture with 22 being ≤ 1 day old. Despite all lambs being < 2 days old, there were 16 instances in which a female moved a lamb from the parturition site before we captured it (Karsch 2014). Average distance for this movement was 162 m (range 5–986 m), and resulted in an average elevation increase of 28 m (range 15–213 m; $SD = 60$ m). None of the individual females fitted with VITs both years of the study used the same parturition site each year; mean distance between

parturition sites from individuals fitted with VITs during both 2012 and 2013 was 3.14 km ($SD = 2.4$ km, median = 2.8 km), with a range of 0.57 km to 9.4 km. Elevation ($t_{12} = -0.146$, $P = 0.887$), slope ($t_{12} = 0.758$, $P = 0.463$), ruggedness ($t_{12} = -0.035$, $P = 0.972$), and visibility ($t_{31} = 0.609$, $P = 0.554$) did not differ at parturition sites of females fitted with VITs both years of the study. There were no areas (i.e., < 400 m) that multiple females used to give birth in a single year. However there were 3 areas that each had 2 parturition sites, 1 from each year, that were within 100 m of each other but all were used by different females. Mean distance between parturition sites located nearest to each other was 1.79 km ($SD = 0.85$ km) and 0.88 km ($SD = 0.15$ km) in 2012 and 2013, respectively. Characteristics of parturition sites of females captured during the second year that were native to the Peloncillo Mountains were similar to those selected by translocated females: elevation ($t_{29} = 1.837$, $P = 0.077$), slope ($t_{29} = -0.007$, $P = 0.995$), ruggedness ($t_{29} = -0.916$, $P = 0.367$), and visibility ($t_{29} = -0.220$, $P = 0.827$). There was no distinction in the spatial distribution of the parturition sites of native and translocated females (Fig. 2).

Four lambs were killed by predators in their first week of life, 1 by a coyote, 1 by a gray fox, and 2 by unknown predators. Overall, mortalities were attributed to pumas ($n = 5$), coyotes ($n = 4$), gray fox ($n = 1$), unknown predators ($n = 2$), and unknown causes ($n = 2$) and all mortalities occurred within 5 months of birth. We did not observe a trend between female age or lamb sex and the mortalities. We censored data associated with the gray fox kill from the analysis because it took place under unusual circumstances outside the study area on a small hill in the middle of the Animas Valley that was atypical of desert bighorn habitat.

There was high model uncertainty among the models predicting the characteristics of a parturition site in comparison to paired random sites (Table 2); however, all 5 top models included slope. Contrary to our prediction that parturition sites would be selected on steeper slopes and in areas of high visibility, the quadratic term (slope²) indicated selection of parturition sites in areas with intermediate slopes and in areas with lower visibility (Table 3). The odds of a site being a parturition site decreased by 6.5% for every 1% increase in visibility. All other odds ratios derived from model-averaged parameter estimates had confidence intervals that included 1.

There was also high model uncertainty for distinguishing between nursery sites and paired random sites and between predation sites and their paired random sites. The top model for distinguishing nursery sites from random sites included linear and quadratic terms for visibility (Table 2). Parameter estimates for the quadratic term for visibility suggested that nursery site selection was higher in areas with high and low visibility and decreased in areas with intermediate visibility (Table 3). Consistent with our predictions, the parameter estimates for slope and ruggedness were positive, but the confidence intervals for the odds ratios included 1. For the predation sites, visibility was the only odds ratio derived from model-averaged parameter estimates with confidence limits

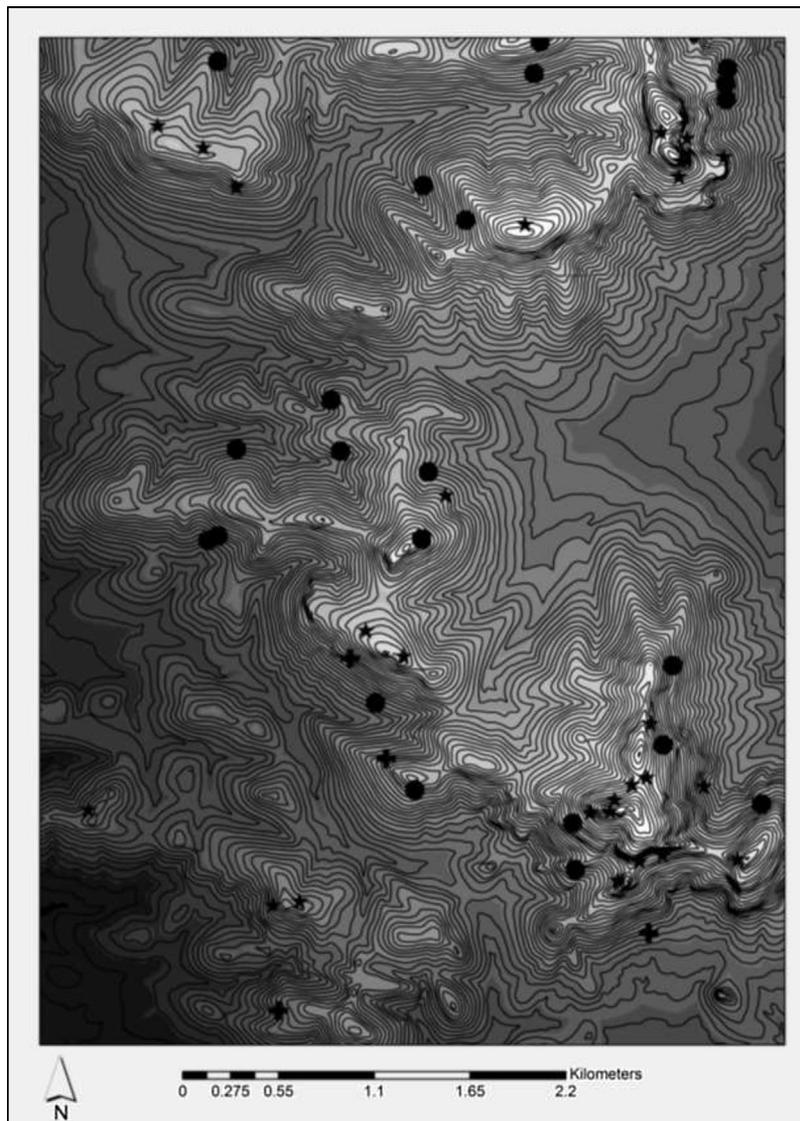


Figure 2. Locations of some of the nursery (black stars) and parturition sites of native (black crosses) and translocated (black circles) desert bighorn sheep in the Peloncillo Mountains, New Mexico, USA during the 2012 and 2013 lambing seasons in relation to elevation (black to white color gradient) and slope (30-m contour lines). Darker colors in the elevation gradient depict the lowest areas; gradient becomes lighter colored with elevation; white areas have the highest elevation.

that did not include 1. Consistent with our predictions, the odds of being a predation site decreased by 17% with every 10% increase in visibility (Table 3).

There was 1 top model for distinguishing between parturition and nursery sites (Table 2), which included linear and quadratic terms for elevation and slope. Contrary to our predictions, there were differences between parturition and nursery sites. The odds of a site being a parturition site rather than a nursery site were highest at intermediate slopes and intermediate elevations (Table 3, Fig. 3).

Elevation, visibility, and their interaction was the highest ranking model distinguishing predation sites from nursery sites, whereas the second highest ranking model had both linear and quadratic terms for elevation and visibility, although both were weakly supported (Table 2). The quadratic terms for elevation and visibility indicated that

the odds of a site being a predation site rather than a nursery site decreased at intermediate elevations and visibility (i.e., were highest at low and high elevations and visibility). These results were only partially consistent with our predictions that predation sites would occur at lower elevations and in areas with low visibility when compared to nursery sites. The interaction of elevation and visibility indicated that predation sites were more likely to occur at lower elevations with lower visibility as compared with nursery sites, and increases in elevation only decreased the odds of a site being a predation site when visibility increased (Fig. 4).

When we examined characteristics at sites where lambs were killed by predators, we found the mean elevation at coyote kills was 270 m lower ($t_7 = -5.22$, $P = 0.001$) than the mean elevation at puma kills. The mean slope at coyote kills was 19.6° less ($t_7 = -2.39$, $P = 0.048$), and the mean

Table 2. Highest ranking a priori models for distinguishing parturition sites, nursery sites, and predation sites from paired random sites, parturition sites from nursery sites, and predation sites from nursery sites for neonatal desert bighorn relative to environmental characteristics in the Peloncillo Mountains, New Mexico, USA during the 2012 and 2013 lambing seasons. We present maximized log likelihoods, number of parameters (K), Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weight (w_i).

Site comparison	Model ^a	-2 Log likelihood	K	AIC_c	ΔAIC_c	w_i
Parturition vs. random	SLOPE + SLOPE ²	34.75	2	38.94	0.00	0.23
	ELEV + SLOPE + ELEV × SLOPE	32.91	3	39.29	0.36	0.19
	SLOPE	38.07	1	40.14	1.20	0.12
	SLOPE + SLOPE ² + VIS + VIS ²	31.85	4	40.50	1.57	0.10
	SLOPE + RUGG + SLOPE × RUGG	34.41	3	40.79	1.86	0.09
Nursery vs. random	VIS + VIS ²	30.02	2	34.27	0.00	0.22
	SLOPE + SLOPE ² + VIS + VIS ²	26.32	4	35.17	0.90	0.14
	ELEV + SLOPE + ELEV × SLOPE	28.78	3	35.28	1.01	0.13
	RUGG	34.50	1	36.58	2.31	0.07
	RUGG + RUGG ² + VIS + VIS ²	27.81	4	36.66	2.39	0.07
Predation vs. random	VIS	13.45	1	15.65	0.00	0.16
	SLOPE	13.87	1	16.07	0.42	0.13
	RUGG	14.39	1	16.59	0.94	0.10
	SLOPE + VIS	12.21	2	16.84	1.19	0.09
	ELEV	15.17	1	17.37	1.73	0.07
Parturition vs. nursery	ELEV + ELEV ² + SLOPE + SLOPE ²	58.81	5	69.94	0.00	0.68
	ELEV	70.60	2	74.81	4.87	0.06
	ELEV + ELEV ²	68.77	2	75.21	5.27	0.05
	ELEV + SLOPE	68.88	3	75.32	5.38	0.05
	ELEV + VIS + ELEV × VIS	36.68	4	45.93	0.00	0.13
Predation vs. nursery	ELEV + ELEV ² + VIS + VIS ²	34.56	5	46.49	0.57	0.10
	ELEV	42.34	2	46.69	0.77	0.09
	SLOPE + RUGG + SLOPE × RUGG	37.79	4	47.04	1.11	0.08
	SLOPE	42.98	2	47.33	1.40	0.07

^a ELEV, elevation; SLOPE, slope; RUGG, ruggedness; VIS, adult female visibility.

visibility was 163% greater ($t_7 = 2.39$, $P = 0.048$) than puma kills (Table 4).

DISCUSSION

Previous reports on the nature of desert bighorn lambing habitat are based almost solely on visual observation of young lambs with their mothers. These reports concluded that parturition and nursery sites occur in areas characterized by steep, rugged terrain, high elevation, and high visibility for enhanced detection of predators (Hansen 1980a, DeForge and Scott 1982, Shackleton et al. 1999). Our results were contrary to these previous reports on desert bighorn, which contend that bighorn use lambing areas in the most precipitous and rugged terrain available (Eustis 1962, Wilson 1980, Geist 1971, Hansen 1980a, DeForge and Scott 1982). Rather, we found that parturition sites were more likely to occur at mid elevations in areas with intermediate slopes than nursery sites. Additionally, we found that parturition sites were widely dispersed, there was no evidence of lambing areas used by multiple females in a single year, nor did we find evidence of site fidelity of individual adult females between years.

As predicted, our habitat selection analysis for nursery and parturition sites indicated that when compared to randomly available locations, the odds of a site being selected for a nursery site increased with slope and odds of a parturition site increased with elevation. However, slope had a quadratic relationship with odds of a site being a parturition site. Although most of the parameter estimates for ruggedness were positive, they were inconclusive because confidence

limits included 1. Given the influence of neonate survival on lifetime reproductive success and fitness of adult female ungulates, selection of parturition and post-parturition habitat is commonly associated with habitat conditions that would reduce predation risk to neonates, which is generally consistent with our results. Other mountain ungulates commonly select steep, high elevation, rocky areas during the post-parturition period after the neonate is more mobile to reduce predation risk (Bon et al. 1995, Grignolio et al. 2007, Côté and Hamel 2007, Festa-Bianchet and Côté 2008). Similarly, ungulates that occupy more gentle terrain select areas where vegetation cover is sufficient to provide cover for neonates (Canon and Bryant 1997, Tull et al. 2001, Ciuti et al. 2006, Bongi et al. 2008).

Contrary to our predictions, selection of parturition sites was negatively associated with visibility, whereas nursery sites were associated with areas of low and high visibility with decreasing odds of use in areas with intermediate visibility. Bangs et al. (2005) reported lower visibility at sites used by desert bighorn females and lambs than random sites and concluded that lower visibility may reduce predator detection by offering more hiding cover when lambs are least mobile and particularly susceptible to predation. Similarly, studies on post-parturition habitat selection of roe deer (*Capreolus capreolus*; Bongi et al. 2008), elk (Rearden et al. 2011, Pitman et al. 2014), mouflon (*Ovis orientalis musimon*; Ciuti et al. 2009), pronghorn (Canon and Bryant 1997), and numerous other species all report use of areas with increased concealment cover for the neonate; however, some studies also report use of areas with increased visibility, allowing the

Table 3. Model-averaged logistic regression coefficient estimates, standard errors, odds ratios, and 90% confidence intervals for odds ratios for variables included in the best approximating models for distinguishing parturition sites, nursery sites, and predation sites from paired random sites, parturition sites from nursery sites, and predation sites from nursery sites for neonatal desert bighorn relative to environmental characteristics in the Peloncillo Mountains, New Mexico, USA during the 2012 and 2013 lambing seasons.

Variable ^a	Model-averaged parameter estimate		Odds ratio	90% confidence limits for odds ratio	
	β	SE		Lower CL	Upper CL
Parturition vs. random					
ELEV	0.026	0.031	1.026	0.975	1.081
SLOPE	0.570	0.271	1.768	1.132	2.760
RUGGED	0.071	0.066	1.075	0.964	1.198
VIS	-0.067	0.001	0.935	0.934	0.936
SLOPE ²	-0.007	0.004	0.992	0.986	0.999
VIS ²	-0.001	0.001	1.001	0.999	1.002
Nursery vs. random					
ELEV	-0.015	0.041	0.958	0.920	1.054
SLOPE	0.311	0.232	1.365	0.932	1.998
RUGGED	0.034	0.041	1.035	0.968	1.106
VIS	-0.183	0.001	0.833	0.832	0.834
SLOPE ²	0.003	0.002	1.003	0.999	1.006
VIS ²	0.002	0.001	1.002	1.001	1.004
RUGGED ²	-0.001	0.001	0.999	0.998	1.001
Predation vs. random					
ELEV	0.329	0.271	1.389	0.889	2.169
SLOPE	-0.019	0.157	0.982	0.759	1.270
RUGGED	0.015	0.143	1.016	0.802	1.286
VIS	-0.016	0.001	0.983	0.984	0.985
Parturition vs. nursery					
ELEV	0.124	0.075	1.132	1.001	1.281
SLOPE	0.341	0.224	1.406	0.972	2.034
ELEV ²	-8.6e-5	3.0e-5	0.999	0.9998	0.9999
SLOPE ²	-0.008	0.004	0.992	0.985	0.999
Predation vs. nursery					
ELEV	-0.044	0.029	0.957	0.912	1.005
SLOPE	-0.086	0.071	0.917	0.816	1.032
VIS	0.079	0.001	1.083	1.082	1.084
ELEV ²	4.2e-5	2.7e-5	1.0004	1.0001	1.0009
RUGGED	-0.057	0.063	0.945	0.851	1.049
VIS ²	0.0013	0.0001	1.001	1.000	1.002

^a ELEV, elevation; SLOPE, slope; RUGG, ruggedness; VIS, adult female visibility.

female to detect approaching predators (Bowyer et al. 1999, Rearden et al. 2011, Pitman et al. 2014).

The spatial scale of our analyses would best be described as the mesoscale. Given the results of previous habitat selection studies on desert bighorn sheep (Krausman et al. 1989, Bleich et al. 1997), it is not surprising that we found that relative to random locations, parturition sites were at intermediate slopes, whereas nursery sites tended to be associated with steeper slopes but the results for nursery sites (vs. random) were inconclusive because of wide confidence intervals. Our selection of paired random locations up to 400 m from the used site would allow for the location of random sites in lower elevations and less rugged areas along the periphery of the mountain. We suggest that the selection of parturition sites occurs at a relatively fine spatial scale. Most parturition sites (31 of 33 sites) were <2 km from the nearest nursery area. The proximity of the parturition and nursery areas would facilitate the isolation of females during parturition and provide relatively easy access to nursery group areas after the lying out period for the lamb was over and the female sought out the safety of the nursery group.

Female bighorn remain secluded with their lambs for only a few days after birth (Constantino 1972, Hansen and Deming 1980); therefore, reports of parturition sites or lambing habitat based on observations of adult females with lambs most likely occurred after the pair left the actual parturition site and joined nursery groups, and do not document birth site locations. Our results suggest that desert bighorn sheep lambs are quite capable of moving up the mountain to steeper and higher elevation nursery group sites within 2–4 days of birth (R. C. Karsch, New Mexico State University, personal observation). Therefore, it is likely that lambing habitat as traditionally defined is really nursery habitat that may not include parturition habitat. More consistent with our findings, Simmons et al. (1963) observed a female and lamb shortly after parturition on Kofa National Wildlife Refuge in Arizona, USA. They described the parturition site as being on gentle terrain that contrasted with bighorn parturition site descriptions in the literature. Similarly, Festa-Bianchet and Côté (2008) reported that only 30% of parturition sites of mountain goats (*Oreamnos americanus*) were on cliffs, the majority were in areas with more gentle terrain that were seldom used by mountain goats during

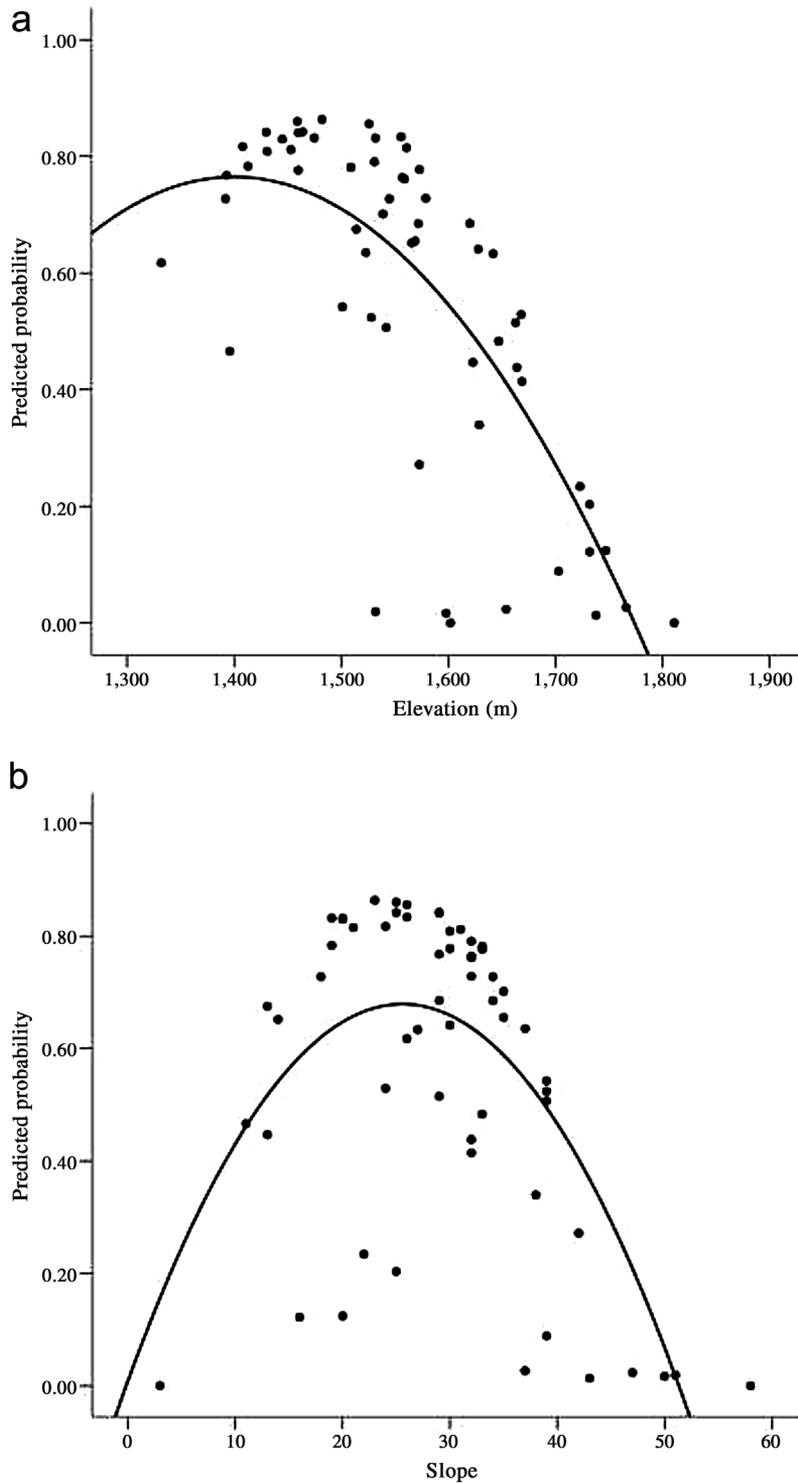


Figure 3. Predicted probability of a site being a parturition site for desert bighorn sheep, estimated from the highest ranking model distinguishing parturition sites from nursery sites in relation to elevation (a) and slope (b) in the Peloncillo Mountains, New Mexico, USA during the 2012 and 2013 lambing seasons.

other times of year. Analogous findings have been reported for elk (Rearden et al. 2011, Pitman et al. 2014), pronghorn (Canon and Bryant 1997), and white-tailed deer (*Odocoileus virginianus*; Huegel et al. 1986).

Eighteen of 26 neonates remained motionless when approached for capture (Karsch 2014). Bighorn are consid-

ered followers using the hider-follower classification of behavior of neonatal ungulates (Lent 1974, Carl and Robbins 1988); however, our results indicate that during the first 2–3 days post-parturition, lambs may be physically unable to make use of rugged terrain (Bangs et al. 2005). Similar 2 to 3-day hiding periods have also been reported for other

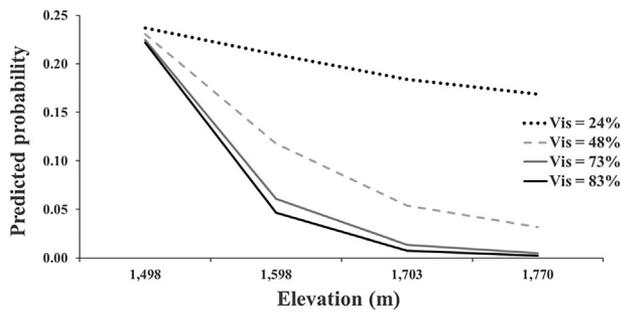


Figure 4. Interaction between elevation and visibility (Vis) in the highest ranking model distinguishing desert bighorn lamb predation sites from nursery sites in the Peloncillo Mountains, New Mexico, USA during the 2012 and 2013 lambing seasons.

mountain ungulates that would typically be considered follower species, including Siberian ibex (*Capra siberica*; Savinov 1962), Daghestan tur (*Capra cylindricornis*; Weinberg 2002), and mountain goats (Festa-Bianchet and Côté 2008). Therefore, spacing away from predators and conspecifics during parturition and using areas with hiding cover may be more important than using rugged, steep terrain that enhances predator evasion for older bighorn. As lambs mature and mobility increases, their survival strategy changes and they and their mother join nursery groups in higher elevation and steeper terrain that defines nursery group habitat.

One possible explanation for selection of areas at intermediate elevations and intermediate slope for parturition sites (vs. nursery sites) is that all females in the first year of the study were newly translocated 3–5 months prior to parturition, and although habitat features were similar to their source range, they were less familiar with the Peloncillo Mountains, causing them to give birth in uncharacteristic terrain. However, we believe this explanation is highly doubtful. Scillitani et al. (2013) reported that translocated alpine ibex (*Capra ibex*), which, like bighorn, are a gregarious mountain ungulate, almost immediately selected the same habitat resources as residents (similar to bighorn sheep in our study) likely because translocated animals were in areas already occupied by residents.

Predation sites tended to occur at both high elevation areas with low visibility and at low elevation areas with moderate visibility when compared to nursery sites. Inconsistencies between our predictions and these results

are likely due to different predator species making kills in areas with different characteristics. Pumas accounted for 50% of predation events, and coyotes accounted for 40%. Pumas and coyotes differ in hunting technique and occupy areas with different habitat conditions, resulting in contrasting habitat characteristics at kill sites. Pumas are a stalking predator (Shaw et al. 2007); therefore, rocky headwalls near the summits of mountains may provide better stalking cover, making lambs susceptible to pumas even at high elevations (Creeden and Graham 1997, Ross et al. 1997). Pumas can contribute to bighorn population declines (Wehausen 1996), in part because they are able to traverse high elevation, steep terrain occupied by bighorn. Coyotes occupy lower elevations with their main prey base being lagomorphs and rodents (Ortega 1987); however, they also prey on neonatal ungulates (Hass 1989, Bleich 1999, Vreeland et al. 2004, Saalfeld and Ditchkoff 2007, Arthur and Prugh 2010). Coyotes have mixed traits of stalkers and coursers (Barber-Meyer and Mech 2008) and are, therefore, less likely to use rugged high elevation habitat where they are less efficient hunters. Unfortunately, small sample sizes precluded separating mortality sites by predator species for statistical analysis; however, locations of coyote-killed lambs were found at lower elevations, on less steep slopes, and in areas with higher visibility than puma-killed lambs. Parturient females may use mid-elevation areas to move away from predators such as coyotes and pumas that travel the valley bottoms and ridgelines, as has been reported for caribou (*Rangifer tarandus*; Bergerud et al. 1984) and moose (*Alces alces gigas*; Bowyer et al. 1999).

This is the first study to present definitive data on the location and characteristics of desert bighorn sheep parturition sites. Additional work in other desert bighorn populations are needed to gain insight into factors affecting parturition site selection and to confirm our results. Understanding parturition site selection and how habitat characteristics at these sites differ from those at predation and nursery sites can provide insight into strategies female bighorn employ during and after parturition to promote lamb survival. Strategies such as isolation prior to parturition, use of lower visibility areas that are mid-elevation during parturition to space away from and avoid predator detection, and movement of young lambs to join nursery groups shortly after birth, may all enhance neonatal bighorn survival in the critical first days and weeks of life.

Table 4. Mean and standard error of elevation (ELEV), slope (SLOPE), ruggedness (RUGGED), and visibility (VIS) at bighorn parturition, nursery, and lamb predation sites in the Peloncillo Mountains, New Mexico, USA in 2012 and 2013.

	Parturition		Nursery		Predation			
					Coyote (n = 4)		Puma (n = 5)	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
ELEV (m)	1523.3	15.1	1610.4	22.2	1389.0	37.7	1659.8	35.2
SLOPE (°)	27.7	1.2	31.6	2.4	11.2	8.0	30.8	3.7
RUGGED	9.1	1.9	19.9	7.9	2.1	0.5	20.4	12.3
VIS (%)	52.1	1.2	48.0	5.0	64.6	8.7	24.5	13.2

MANAGEMENT IMPLICATIONS

Numerous management agencies have seasonal closures in place to reduce disturbance to particular desert bighorn sheep populations during the lambing season through trail closures to restrict human activity or livestock exclusion (Gallizioli 1977, Acheson 2005, Upchurch 2013). If our findings that parturition sites are at intermediate slopes and elevations compared to nursery areas, then agencies that have active management plans to reduce disturbance during lambing season could consider extending areas closed during the lambing season to include lower elevation and less steep habitat to minimize disturbance to desert bighorn at parturition sites and enhance desert bighorn reproductive success.

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