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Featured Article

Survival and Cause-Specific Mortality of Desert Bighorn Sheep Lambs

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ABSTRACT Juvenile recruitment in desert bighorn sheep (*Ovis canadensis mexicana*) is highly variable, yet the mechanisms influencing neonate survival are not well understood. Because few studies have equipped desert bighorn sheep lambs with telemetry collars, definitive data on cause-specific mortality, and lamb survival estimates are lacking. Our objectives were to estimate lamb survival rates and determine cause-specific mortality for desert bighorn sheep lambs during a period of mountain lion (*Puma concolor*) and coyote (*Canis latrans*) removal in southwestern New Mexico, USA. We captured pregnant adult females each fall and fitted them with a telemetry collar and a vaginal implant transmitter to aid with neonate captures. We captured and radio-collared 12 desert bighorn sheep lambs in 2012 and 14 in 2013 within 48 hours of parturition in the Peloncillo Mountains, New Mexico. We estimated lamb survival to 6 months of age. Across both years there were 14 mortalities, 12 of which were due to predation. Mountain lions killed 5 lambs (2 in 2012 and 3 in 2013), coyotes killed 4 lambs (all in 2013), a gray fox (*Urocyon cinereoargenteus*) killed 1 lamb in 2012, and 2 lambs were killed by unknown predators in 2013. Staged-based survival estimates indicated the highest mortality rates occurred in the first week post birth; 5 of 14 lamb mortalities occurred before 7 days of age. Lamb survival to 6 months was substantially lower in 2013 (0.20 ± 0.11 [SE]) than in 2012 (0.71 ± 0.14) with the differences in survival attributed to increased coyote predation in 2013. We did not detect differences in body mass at birth between years or differences in body mass, chest girth, or neck circumference at birth between lambs that were killed by predators and those that survived. Coyotes, mountain lions, and the gray fox killed lambs <8 weeks of age, but only mountain lions killed lambs >8 weeks old. Predator removals focused around the parturition period of desert bighorn sheep may be more likely to influence lamb survival rates than removals outside of the lambing season.

KEY WORDS coyote predation, desert bighorn sheep, juvenile recruitment, lamb survival, mortality, mountain lion predation, *Ovis canadensis mexicana*, vaginal-implant transmitter.

Neonate survival is the primary demographic rate affecting population growth in ungulates when adult survival is high and relatively constant (Gaillard et al. 1998, 2000; Raithel et al. 2007). Juvenile survival rates have high interannual variability, particularly in ungulates inhabiting arid and semi-arid environments (Leopold and Krausman 1991, Lawrence et al. 2004, Simpson et al. 2007, McKinney et al. 2008). High adult survival and variable juvenile survival often characterize desert bighorn sheep (*Ovis canadensis mexicana*) populations (Rubin et al. 2000, Wehausen 2005, McKinney et al. 2006*a*). Despite high pregnancy and birth rates (e.g., >90% of breeding age females produce one lamb each year; Etchberger and Krausman, 1999, Overstreet 2014), juvenile recruitment in desert bighorn is extremely variable and often low (e.g., <0.20; Bradley and Baker 1967, Hansen 1967, DeForge and Scott 1982, Douglas and Leslie 1986, Douglas 2001). Previous work has implicated a strong link between precipitation, particularly fall and winter rainfall, and juvenile recruitment in desert bighorn sheep populations (Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001, McKinney et al. 2001). Few studies, however, have equipped desert bighorn lambs with telemetry collars and data on cause-specific mortality and estimates of lamb survival are lacking for most populations (Krausman and Shackleton 2000, Parsons 2007).

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Few published studies report neonatal survival of bighorn sheep based on monitoring lambs with telemetry collars (Hass 1989, Etchberger and Krausman 1999, Goldstein 2001, DeForge 2002, Smith et al. 2014*a*). Many studies used helicopters to locate and capture lambs when they were >1–3 weeks old (DeForge 2002, Parsons 2007). Survival estimates from such studies are likely biased high because neonatal lambs that die prior to capture efforts are not available for sampling (Gilbert et al. 2014). When using a short but intensive capture period, catching a sufficient number of neonates soon enough (i.e., 24–48 hr) after birth for a relatively unbiased sample for estimating lamb survival is more feasible for northern species or subspecies of mountain sheep because of their relatively short and synchronous lambing season (Scotton and Pletscher 1998, Arthur and Prugh 2010). In contrast, desert bighorn lambing seasons are extended over several months (Bunnell 1982, Hass 1997); thus, capture efforts concentrated over a short time period would result in small sample sizes and lambs being various ages at time of capture. To obtain an unbiased sample of desert bighorn sheep neonates for survival estimation, capture efforts will necessarily be protracted. Thus, the use of alternative methods (e.g., vaginal implant transmitters) are important to capture and monitor a representative sample of neonatal desert bighorn sheep.

At least 14 mountain ranges in New Mexico, USA, were formerly occupied by desert bighorn sheep (New Mexico Department of Game and Fish [NMDGF] 1995, 2003). By the 1950s only populations in the San Andres and Big Hatchet mountains were extant. Historical population declines were attributed to a combination of disease transmission from livestock (e.g., domestic sheep), uncontrolled hunting, drought, and competition with livestock (Buechner 1960, NMDGF 2003). More recent threats to the persistence of desert bighorn in New Mexico include drought, extensive livestock grazing, fire suppression, and increased mountain lion (*Puma concolor*) predation (NMDGF 2003). Desert bighorn were listed as an endangered species in New Mexico in 1980 (NMDGF 1995, 2003). Following an intensive management program by the NMDGF that included captive-breeding, translocation (both captive bred and wild), mortality monitoring, and mountain lion control, the recovery criteria for removal from the state's endangered species list were met in 2010 (Goldstein and Rominger 2011). Desert bighorn sheep were removed from the state's threatened and endangered species list in 2011. Although reducing mountain lion predation and monitoring adult mortality has been a component of desert bighorn recovery and management in New Mexico, estimates of lamb survival, recruitment, and cause-specific mortality could contribute to more effective management of desert bighorn sheep. Our specific objectives were to estimate lamb survival rates and determine causes of mortality during a period of mountain lion and coyote removal.

STUDY AREA

The Peloncillo Mountains run northwest for approximately 120 km from the United States–Mexico border in southwestern New Mexico, and are flanked by the Animas Valley and Animas Mountains to the east and the San Simon Valley and Chiricahua Mountains in Arizona to the west. The United States Forest Service manages much of the southern Peloncillo Mountains, whereas the majority of the northern portion of the range is managed by the Bureau of Land Management interspersed with state trust lands and private land. Our study area (~83 km^2) was located in the central portion of the range, west of Animas, New Mexico.

Long-term (1960–2013) mean annual precipitation was 28.2 cm (SD = 8.94 cm; National Oceanic and Atmospheric Administration [NOAA] 2015; Animas, NM ~10 km east of the study area), with the majority (54%) falling from July to September (Western Regional Climate Center [WRCC] 2012). Total precipitation in 2011 was 15% above average (32.3 cm) but was 43% and 46% below average in 2012 and 2013, respectively. Long-term mean total precipitation during late gestation (Nov–Dec) is 3.7 cm. Total rainfall during late gestation in 2011 was 11.3 cm, whereas during late gestation in 2012 only 1.2 cm (32% of average) of rain was recorded. Mean total precipitation during the period from lambing through weaning (Jan–Jun) is 6.3 cm; total precipitation during this time period was 4.5 cm (71% of average) and 4.6 cm (72% of average) in 2012 and 2013, respectively (NOAA 2015). Maximum temperatures occurred June–August with an average daily high temperature of 34.2°C and a low of 16.8°C. Minimum monthly temperatures occurred December–February with an average daily high of 15.2°C and low −1.6°C (WRCC 2012).

Common vegetation types included semi-desert grassland and Chihuahuan desert scrub at lower elevations (<1,500 m; Dick-Peddie 1993, Brown 1994). Common woody plants were mariola (*Parthenium incanum*), whitethorn acacia (*Vachellia constricta*), and juniper (*Juniperus monosperma*); dominant grasses included tobosa (*Pleuraphis mutica*), black grama (*Bouteloua eriopoda*), and sixweeks threeawn (*Aristida adscensionis*). Succulents included sotol (*Dasylirion wheeleri*), prickly pear (*Opuntia engelmannii*), and cane cholla (*Cylindropuntia spinosior*). Caliche globemallow (*Sphaeralcea laxa*), woolly plantain (*Plantago patagonica*), Rothrock's crownbeard (*Verbesina rothrockii*), and Gordon's bladderpod (*Physaria gordonii*) were abundant forbs.

Other wild ungulates in our study area included collared peccary (*Pecari tajacu*) and mule deer (*Odocoileus hemionus*). Domestic cattle were common on all grazing allotments in and around the study area. Predators present in the study area included mountain lions, bobcats (*Lynx rufus*), coyotes, gray foxes (*Urocyon cinereoargenteus*), and golden eagles (*Aquila crysaetos*).

The NMDGF began mountain lion removal in the Peloncillo Mountains in 2001 and continued throughout the duration of this project. In addition, the Department of Agriculture's Animal Plant and Health Inspection Service's Wildlife Services (USDA-APHIS) had an active coyote removal program in grazing allotments in the Peloncillo Mountains during our study. Five mountain lions were removed from the Peloncillo Mountains in 2012: February (during the lambing season, $n = 1$), March ($n = 2$), May ($n = 1$), and October ($n = 1$). In addition, 2 mountain lions were removed in 2013, 1 just south of the study area in March and 1 in the study area in May after it killed 2 lambs in 2 days. The USDA-APHIS removed 34 coyotes in 2011, 19 in 2012 (1 during the lambing season from Jan–Apr), and 69 in 2013 (38 during the lambing season; A. May and R. C. Fajardo Jr., USDA APHIS, personal communication).

METHODS

In November 2011, we captured pregnant adult female desert bighorn in the Fra Cristobal Mountains ($n = 11$) and the Red Rock Wildlife Area ($n = 10$) using a net gun fired from a helicopter (Krausman et al. 1985). We translocated animals and released them in the Peloncillo Mountains. In December 2012, we captured 21 adult females in the Peloncillo Mountains using similar methods. One female translocated to the Peloncillo Mountains in 2011 moved to the Pyramid Mountains (~25 km northeast of the Peloncillo Mountains) and was captured in 2012 and released back in the Peloncillo Mountains. We flew all animals to a nearby processing station where we determined pregnancy status using a portable ultrasound (Sonosite Vet 180 Plus, Oceanside, CA, USA). We fitted pregnant animals ($n = 39$; 20 in 2011 and 19 in 2012) with a uniquely colored, very high frequency (VHF) radio-collar with a 6-hour mortality sensor (2011, model 2520B, Advanced Telemetry Systems [ATS], Isanti, MN, USA; 2012, model V5C 181C, Sirtrack, North Liberty, IA, USA), a uniquely colored and numbered ear tag, and a vaginal implant transmitter (VIT; model PETTMPF2, ATS). All animal capture and handling procedures followed acceptable methods and were approved by the New Mexico State University Institutional Animal Care and Use Committee (IACUC protocol 2011-026; Sikes et al. 2016). The NMDGF conducted a helicopter survey in May 2011, prior to translocation of bighorn into the Peloncillo Mountains, and estimated the total population to be 95–110 individuals (NMDGF 2014); therefore, with the newly translocated females, study animals made up approximately 40% of the adult female population.

Starting in December each year, we monitored VIT frequencies daily. When the temperature switch was activated during parturition, the VIT transmitted a binary series of pulses that we used to calculate amount of time the VIT had been expelled to within 0.5 hours. We then used the time of VIT expulsion to estimate birth date and age at capture. When we detected an expelled VIT, we immediately attempted to visually locate the adult female through a spotting scope from a distance >500 m to observe her behavior and search for a nearby lamb. When we found a lamb, 1 person monitored the female and lamb through the scope while 2 people approached to capture the lamb (Smith et al. 2014*b*, Karsch et al. 2016). If we did not find a lamb where we observed the adult female, we used a directional antenna to locate the VIT. We then searched the area around the VIT and between the adult female's location and the VIT to look for the lamb and to confirm a parturition event (e.g., presence of blood, birthing fluids). Upon capture, we blindfolded the lamb and fit it with an expandable VHF collar equipped with a 6-hour mortality switch (Model M4210, ATS). We inserted a uniquely numbered ear tag, and recorded sex and morphometric measurements (i.e., weight [kg], neck circumference [cm], and chest girth [cm]) and tooth eruption status. Handling time was ≤15 minutes, and we released lambs at site of capture (Karsch 2014). We continued monitoring the lamb via spotting scope after release to determine if it reunited with its mother.

We monitored lambs daily from capture until 16 weeks of age, then every 2–4 days until 6 months of age and weekly thereafter until death, age 1, or the collar dropped off. When we detected a mortality signal, we located and examined the carcass and searched the surrounding area within 100 m of the carcass to determine cause of death. We recorded mortality site coordinates, a site description, carcass condition (e.g., intact, partially, or completely consumed), and evidence of prior injuries or disease. We performed a necropsy and sent samples of heart, kidneys, lungs, and liver to the Veterinary Diagnostic Services Laboratory in Albuquerque, New Mexico, for further analysis when the carcass was sufficiently fresh and cause of death was not apparent. Carcass and site characteristics indicative of mountain lion kills included mountain lion tracks, scrapes, or scat at the cache site, vegetation, or other debris covering the carcass, subcutaneous hematomas with 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). We distinguished coyote and fox kills from mountain lion kills, and from each other, based on canine puncture spacing (2.9–3.5 cm for coyotes, and 1.27–2.54 cm for foxes) and tracks at the site (Bowns 1995). Scavenging was distinguished from predation by the presence of subcutaneous hematomas and associated canine puncture wounds. We classified the cause of mortality as unknown, if we could not definitively determine the cause.

Data Analysis

Because neonate birth mass and body size can be related to survival, we used multivariate analysis of variance to examine differences in body mass, chest girth, and neck circumference by year. We also determined if there were differences in morphological characteristics between lambs that survived and those that died during our study.

We used the nest-survival model in Program MARK (White and Burnham 1999) to estimate bighorn lamb survival rate until 26 weeks of age and to assess changes in survival as lambs aged. We used the nest-survival model because it is the most appropriate for ragged telemetry data (e.g., variable intervals between relocations; Dinsmore et al. 2002, Rotella 2007, Devineau et al. 2014). We modeled survival to 26 weeks because most of the collars fell off within that period, or the animals died.

We first compared models exploring differences in survival rates to 26 weeks between years to those that assumed constant survival rates across years using Akaike's Information Criterion corrected for sample size (AIC_c). When we examined differences in survival rates to 26 weeks between years, there was more support for year-specific survival rates,

(AIC_c weight = 0.993) than for constant survival over both years (AIC_c weight = 0.007; $\Delta AIC_c = 9.83$). Thus, all subsequent analyses were year-specific. During each year, we explored stage-specific differences in survival rate using 7 *a priori* models of varying age intervals. Age intervals allow for survival rate estimation for specific biologically meaningful time intervals based on growth and development of young and have been examined with young grizzly bears (*Ursus arctos*; Schwartz et al. 2006), elk (*Cervus canadensis*; Barber-Meyer and Mech 2008), mule deer (Heffelfinger et al. 2018), and white-tailed deer (*Odocoileus virginianus*; Grovenburg et al. 2011). We used stage-specific intervals similar to those in Smith et al. (2014*a*) in their survival estimation for Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) lambs in South Dakota, USA. We examined week 1 separately for most models because it is typically the period of highest neonatal mortality in ungulates (Vreeland et al. 2004, Grovenburg et al. 2011). We staged models as follows: 1) a null model that examined constant weekly survival to 26 weeks; 2) a model that examined survival to 26 weeks with varying weekly survival; 3) a 2-stage model in which lamb survival varied between <1 week and >1 week post-birth; 4) a 3-stage model in which lamb survival varied among 1 week, 2–4 weeks, and >4 weeks post-birth; 5) a 3-stage model in which lamb survival varied among 1 week, 2–8 weeks, and >8 weeks post-birth; 6) a 3-stage model in which lamb survival varied among 1–2 weeks, 3–8 weeks, and >8 weeks post-birth; and 7) a 4-stage model in which lamb survival varied among 1 week, 2–4 weeks, 5–8 weeks, and >8 weeks post–birth.

We calculated survival rates for time periods by exponentiating daily survival rates with the number of days in the time period. We estimated survival over the 26-week period by multiplying period-specific estimates. We calculated standard errors for each stage and over the entire 26-week period using a version of the delta method (Seber 1982, Powell 2007). We used an information-theoretic approach to rank models using AIC_c (Burnham and Anderson 2002). We considered models with ΔAIC_c values ≤ 2.0 to be competing models and models between 2 and 7 to have some support (Burnham and Anderson 2002). We also considered model weight to further examine relative model support.

RESULTS

In 2011, all 21 adult females we captured in the Fra Cristobal Mountains and Red Rock Wildlife Area were pregnant (100% pregnancy rate). One adult female captured in Red Rock Wildlife Area died during capture, and we released the remaining 20 pregnant females in the Peloncillo Mountains. Three females died prior to parturition and the remaining 17 females all successfully gave birth. In 2012, we captured 21 adult females, 19 of which were pregnant and 1 had given birth just prior to the capture (pregnancy rate 95%). The only female captured in the Peloncillo Mountains in 2012 that was not pregnant was estimated to be >11 years old based on previous captures by NMDGF in 2003 and 2007. The female that moved to the Pyramid Mountains was not pregnant; however, there are no known male desert bighorn sheep in the Pyramid Mountains (E. M. Rominger, NMDGF, unpublished data). Of the 39 pregnant females captured, we captured 14 individual adult females during both years, resulting in 25 unique adult females captured in 2 years.

We captured 26 lambs from the surviving adult females with VITs: 12 of 17 in 2012 and 14 of 19 in 2013. We captured lambs from 18 individual females; for 8 females we captured their lamb in both years. All lambs were ≤ 48 hours old at capture. Lamb sex ratios were 42:58 (female:male) in 2012 and 43:57 in 2013.

We documented 14 lamb mortalities during the 26-week monitoring period, 3 in 2012 and 11 in 2013. Predation was the leading cause of mortality ($n = 12$). Across both years, 5 lamb mortalities occurred when lambs were ≤ 7 days of age, and 7 of all mortalities occurred during the first month of life. Mountain lions killed 5 lambs (2 in 2012 and 3 in 2013), coyotes killed 4 lambs (all in 2013), a gray fox killed 1 lamb in 2012, and 2 lambs were killed by undetermined predators in 2013. In 2013, 1 lamb died of unknown causes and 1 lamb was suspected to have died as a result of abandonment. The lamb killed by the gray fox was born in the Pyramid Mountains, which is atypical bighorn habitat, after its dam moved from the Peloncillo Mountains just prior to parturition. Lambs killed by coyotes during our study were 5, 32, 43, and 47 days old, whereas mountain lions killed lambs at 22, 36, 92, 120, and 136 days of age. Tissue samples showed no evidence of disease for the lamb that died of unknown cause or for the abandoned lamb.

There was no difference in mean body mass of lambs between years ($F_{1,\ 21} = 0.169$, $P = 0.688$). However, neck circumference was on average 1.5 cm (95% CI = 0.54–2.4 cm; $F_{1,\ 21} = 11.90$, $P = 0.004$) larger and chest girth was 4.1 cm larger (95% CI = 1.02–7.23; $F_{1,21} = 8.22$, $P = 0.013$) in 2012 than in 2013. There was no difference in body mass ($F_{1,\ 21} = 0.550$, $P = 0.472$), chest girth ($F_{1,\ 21} = 1.62$, $P = 0.225$), or neck circumference ($F_{1,\ 21} = 1.71$, $P = 0.213$) between lambs that were killed by predators and those that survived until 26 weeks of age. Mean body mass of males was 3.86 ± 0.29 kg (SE), 3.84 ± 0.19 kg, and 4.32 ± 0.31 kg for those that survived, were killed by coyotes, or were killed by lions, respectively. Mean body mass of females that survived, were killed by coyotes, or killed by lions was 3.39 ± 0.26 kg (SE), 2.80 ± 0 kg ($n = 1$), and 3.75 ± 0.43 kg, respectively.

We censored the abandoned lamb from the survival analysis because it may have been abandoned as a result of capture. The top-ranked stage-specific models of survival to 26 weeks differed between years. In 2012, survival rates were high and there was considerable model uncertainty with 5 competitive models ($\Delta AIC_c \leq 2$; Table 1). The top model had 2 stages of survival with a survival estimate of 0.90 ± 0.09 for the first week, and a weekly survival rate after week 1 of 0.99 ± 0.01. Estimated survival from this model over the 26 weeks was 0.71 ± 0.14. The second-ranked model had age stages of the first week, weeks 2–8, and >8 weeks. Weekly survival rates during time intervals in this model were 0.90 ± 0.09, 1.0 ± 0.0, and 0.99 ± 0.01, respectively; there were no mortalities in weeks 2–8. Estimated survival to 26 weeks from this model was 0.69 ± 0.16.

Table 1. *A priori* staged models used to estimate desert bighorn lamb survival (S) by age interval in the Peloncillo Mountains, New Mexico, USA, for the 2012 and 2013 lambing seasons. We present Akaike's Information Criterion adjusted for small sample size (AIC_c), ΔAIC_c, Akaike weight, number of parameters (K), and deviance.

Model[a]	AIC_c	ΔAIC_c	Weight	K	Deviance
2012					
$S_{1\text{ wk},\ >1\text{ wk}}$	44.738	0.000	0.265	2	40.720
$S_{1\text{ wk},\ 2–8\text{ wks, and }>8\text{ wks}}$	45.165	0.437	0.213	3	39.149
$S_{(.)}$	45.252	0.524	0.204	1	43.250
$S_{1\text{ wk},\ 2–4\text{ wks},\ >4\text{ wks}}$	46.137	1.408	0.131	3	40.121
$S_{1–2\text{ wks},\ 3–8\text{ wks, and }>8\text{ wks}}$	46.514	1.786	0.109	3	40.498
$S_{1\text{ wk},\ 2–4\text{ wks},\ 5–8\text{ wks, and }>8\text{ wks}}$	47.176	2.447	0.078	4	39.149
S_{wk}	83.751	39.022	0.000	26	30.792
2013					
$S_{1\text{ wk},\ 2–8\text{ wks, and }>8\text{ wks}}$	103.944	0.000	0.370	3	97.912
$S_{1\text{ wk},\ 2–4\text{ wks},\ 5–8\text{ wks, and }>8\text{ wks}}$	104.613	0.670	0.265	4	96.560
$S_{1–2\text{wks},\ 3–8\text{ wks, and }>8\text{ wks}}$	105.000	1.056	0.218	3	98.968
$S_{1\text{ wk},\ >1\text{ wk}}$	107.055	3.111	0.078	2	103.039
$S_{(.)}$	108.408	4.465	0.040	1	106.403
$S_{1\text{ wk},\ 2–4\text{ wks},\ >4\text{ wks}}$	109.034	5.091	0.029	3	103.002
S_{wk}	141.441	37.498	0.000	26	87.518

[a] wk = weeks post-parturition.

In 2013, there were 3 competing models (Table 1). For the top model, estimated survival over the first week was 0.74 ± 0.13, whereas weekly survival estimates for weeks 2–8 and >8 weeks were 0.87 ± 0.05 and 0.98 ± 0.02, respectively. The second-ranked model provided a further refinement of survival between the second and eighth week. For the second-ranked model, weekly survival estimates for each time interval were 0.74 ± 0.1 (week 1), 0.92 ± 0.05 (weeks 2–4), 0.81 ± 0.07 (weeks 5–8), and 0.98 ± 0.02 (>8 weeks), indicating that in 2013, survival was lowest in week 1, and lower in weeks 5–8 than during weeks 2–8 and >8 weeks. Overall survival to 26 weeks in 2013 ranged between 0.20 ± 0.11 for the top model to 0.18 ± 0.11 when considering model-averaged estimates from the top 3 models.

DISCUSSION

Substantial annual variation in neonate survival is commonly reported in studies of ungulates inhabiting arid environments including desert bighorn sheep (Rubin et al. 2000, Wehausen 2005, McKinney et al. 2006*a*), mule deer (Leopold and Krausman 1991, Lawrence et al. 2004), and pronghorn (*Antilocapra americana*; Simpson et al. 2007, McKinney et al. 2008). Similarly, we found that desert bighorn lamb survival varied greatly between the 2 years of our study. Mountain lion predation was the most common cause of mortality for desert bighorn lambs during both years of our study despite active mountain lion control efforts. Lambs may be particularly vulnerable to mountain lion predation, even in areas of escape terrain (Karsch et al. 2016). This increased vulnerability of lambs to mountain lions may in part explain consistent mountain lion predation during both years of our study. Additionally the timing of mountain lion removals are likely more critical in determining whether or not removals result in reduced predation on neonates compared to adult desert bighorn sheep.

Coyote predation accounted for the largest difference in mortality sources between the 2 years of our study, with no lambs being killed by coyotes in 2012 and 4 killed in 2013. The USDA-APHIS conducted coyote removal in and around the Peloncillo Mountains during our study. Although 38 coyotes were removed during the 2013 lambing season, 35 of 38 coyotes removed were not removed until after 3 of 4 coyote predation mortalities had already occurred. Some studies have reported that coyote removal immediately preceding and following ungulate birthing seasons has resulted in increased recruitment, but others reported that effects of coyote removal on recruitment could be variable (Smith et al. 1986, Hurley et al. 2011, Kilgo et al. 2014, Gulsby et al. 2015).

Mountain lions have been previously reported to contribute to desert bighorn population declines or hamper recovery efforts (Hayes et al. 2000, Kamler et al. 2002, Rominger et al. 2004, McKinney et al. 2006*b*, Rominger 2018). For example, mean annual cause-specific mortality rates for adult females from mountain lion predation in the Peloncillo Mountains was 0.22 during periods without management removal of mountain lions (1997–1999; 2000–2002) and declined to 0.05 during periods with an active mountain lion removal program (1999–2000, 2002–2011; Goldstein and Rominger 2012). Furthermore, mortality rate from causes other than lion predation was 0.03 during periods without lion removals and 0.04 when lion removals were being conducted; thus, mountain lion predation was likely additive for adult desert bighorn sheep. However, data on lamb survival and cause-specific mortality for desert bighorn lambs is not available for periods in the absence of mountain lion control efforts. Thus, it is unclear if and when mountain lion predation on desert bighorn lambs is additive, partially additive, or compensatory.

Numerous studies report predation as the main proximate cause of mortality for mountain sheep lambs (Hass 1989, Goldstein 2001, Arthur and Prugh 2010, Smith et al. 2014*a*). However, only 3 studies have reported data derived from fitting desert bighorn lambs with radio-collars (Etchberger and Krausman 1999, DeForge 2002, Parsons 2007). Parsons (2007) fit 21 lambs, ranging in age from <1 to

71 days, with telemetry collars, 11 of which died; 5 were killed by mountain lions, and 3 by golden eagles. DeForge (2002) reported that mortalities of desert bighorn sheep lambs 18–70 days old in the Santa Rosa Mountains, California, USA, were attributed to bobcat (21%), coyote (29%), and mountain lion (7%) predation. Lamb mortality studies on Dall's (*Ovis dalli*; Arthur and Prugh 2010) and Rocky Mountain bighorn sheep (Hass 1989, Goldstein 2001, Smith et al. 2014*a*) also report predation as the main cause of mortality. Arthur and Prugh (2010) captured 119 Dall's sheep lambs, of which 80 died of known causes with 93% of mortalities attributed to predation, primarily by coyotes (45%) and golden eagles (34%). Rocky Mountain bighorn lamb predation mortalities have been attributed to coyotes, mountain lions, bobcats, and golden eagles (Hass 1989, Goldstein 2001, Bleich et al. 2004). We found that a similar suite of predators were responsible for predation of desert bighorn lambs in our study, but almost all predation events were due to mountain lions and coyotes. We did not document any mortalities due to golden eagle predation, despite their regular presence in our study area. In addition, predation of desert bighorn sheep lambs by gray fox, as observed during our study, has not been previously reported.

Although predation was the leading proximate cause of mortality during this study, variable precipitation may have contributed to differences in 6-month survival rates between years. Forage production and nutritional content in arid systems are determined largely by precipitation patterns (Noy-Meir 1973, Krausman et al. 1989, Marshal et al. 2005, Cain et al. 2017). The effect of rainfall on forage growth influences forage quality and maternal body condition, which in turn can influence population performance. Neonate survival can be influenced by maternal body condition with young born to females in good nutritional condition typically having higher birth mass and post-parturition growth rates. Neonates that are heavier at birth typically have higher survival rates that those born lighter (Thorne et al. 1976, Fairbanks 1993, Keech et al. 2000, Cook et al. 2004, Heffelfinger et al. 2018). Several studies have reported a positive relationship between fall lamb:adult female ratios in desert bighorn sheep and rainfall during the previous winter period (Douglas and Leslie 1986, Wehausen et al. 1987, Douglas 2001, Wehausen 2005, Longshore et al. 2016), suggesting a link between rainfall during late gestation and early post-parturition, and juvenile recruitment. Rainfall during the second year of our study when we observed very low lamb survival (i.e., 20%) was 68% below average compared to the first year when lamb survival was around 70% and rainfall during late gestation was almost 3 times higher than normal. If the difference in precipitation affected maternal condition and subsequently the size of lambs at birth resulting in lower survival, we would have expected to observe smaller lambs during the second year with only the larger lambs surviving through our monitoring period. Yet, we did not find substantial differences in birth mass of lambs between years nor did we find differences in body size between surviving and non-surviving lambs.

Precipitation and forage may have indirectly affected lamb survival through changes in maternal habitat selection to compensate for poorer forage conditions during the low rainfall year. Coyotes typically occupy lower elevations with their main prey being lagomorphs and rodents (Clark 1972, Ortega 1987). Below-average precipitation in late 2012 and early 2013 may have reduced the abundance of lagomorphs and rodents (Ernest et al. 2000, Hernández et al. 2011) causing coyotes to seek alternative prey (Arthur and Prugh 2010). McKinney and Smith (2007) reported that coyotes in the Sonoran Desert ate more large prey items during winter drought. In addition, during periods with good foraging conditions, adult female desert bighorn sheep may be able to obtain high-quality diets in areas near escape terrain, reducing coyote predation risk for neonates. During years of low nutrient availability associated with below-average rainfall, adult female desert bighorn sheep may forage farther from escape terrain to increase nutrient intake, potentially exposing lambs to higher predation risk due to coyotes in the less rugged terrain. Unfortunately, sufficient location data on the adult female desert bighorn sheep in our study are not available to assess differences in foraging areas in relation to rainfall. However, coyote predation sites were in areas with lower elevation, with less rugged terrain and lower slopes than parturition sites, nursery sites, or mountain lion kill sites (Karsch et al. 2016). In multi-predator systems, variation in species-specific hunting strategies compounded with indirect effects of forage conditions can result in a cumulative negative effect on neonate survival (Gustine et al. 2006, Duquette et al. 2014).

During our study, 1 of 3 (2012) to 4 of 11 (2013) of all lamb mortalities occurred before 7 days of age. Therefore, survival studies based on bighorn lambs captured after the first week of life likely produce survival rates that are biased high (Gilbert et al. 2014). We documented the majority (79%) of mortalities during the first 8 weeks of life, and 21% occurred between 8 and 26 weeks, similar to reports from many other studies on neonatal ungulates (Hass 1989, Gustine et al. 2006, Arthur and Prugh 2010, Grovenburg et al. 2011, Smith et al. 2014*a*). Coyotes and mountain lions killed lambs that were <8 weeks old; however, only mountain lions killed older animals. Therefore, some previous studies may not have detected significant coyote predation because they collared older lambs. Future efforts to estimate desert bighorn lamb survival should strive to capture neonates <2 days old to provide less biased estimates of lamb survival and cause-specific mortality. Recent technological development in VITs with remote communication (i.e., satellite, cellular) capabilities should aid in monitoring pregnant desert bighorn sheep in remote, rugged, and inaccessible areas and facilitate capture of desert bighorn neonates.

Much of our data were collected from lambs born to females recently translocated to the Peloncillo Mountains. This may raise concerns regarding how representative our data are of survival of lambs born to resident females given that translocated animals often have lower vital rates during an acclimation period after translocation (McKinney et al. 2006*b*). Our data, however, do not support the idea that

Figure 1. Male lamb born 27 February 2012 and captured <48 hours after parturition in the Peloncillo Mountains, New Mexico (top panel; Photo by R.C. Karsch, New Mexico State University). The same animal photographed during aerial surveys in the Peloncillo Mountains in spring 2017 (lower panel; photo by N.M. Tatman, New Mexico Department of Game and Fish).

naiveté of these translocated females had a large effect on lamb survival in our study. First and most importantly, the 6-month lamb survival rate was nearly 70% the first year after the sheep were released and all study animals were translocated animals. If the sheep were naïve, and this affected lamb survival, we would expect to have lower survival the first year after translocation, not the second year as we observed. In addition, there were no differences in distribution, parturition site characteristics, or nursery habitat use between those animals that were translocated and those that were resident during our study (Karsch et al. 2016). Thus, we found little evidence that would indicate that translocation influenced lamb survival during our study.

MANAGEMENT IMPLICATIONS

Mountain lion removal could provide protection to desert bighorn sheep year round because sheep remain vulnerable at all ages. The period when desert bighorn lambs are vulnerable to coyote predation is generally much shorter than for mountain lions. Improving survival rates of desert bighorn sheep lambs could contribute to increased population performance, and enhance wildlife viewing and recreational opportunities (Fig. 1). To improve survival rates of desert bighorn sheep lambs, managers may consider focusing predator removal efforts immediately prior to and during the lambing season because lambs that survive the first 2 months of life have a higher chance of avoiding predation, particularly from coyotes. However, the protracted lambing season of most desert bighorn sheep populations would complicate implementing a targeted coyote removal effort that would coincide with the period that desert bighorn lambs are most vulnerable, and would be more difficult than with species with a more synchronous birth pulse. In addition, studies that fail to capture desert bighorn lambs near parturition will likely produce biased survival estimates and inaccurate appraisals of primary causes of mortality due to early mortality of lambs.

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