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# Survival of Female Bighorn Sheep (*Ovis canadensis*) in the Black Hills, South Dakota

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**ABSTRACT.**—Bighorn sheep (*Ovis canadensis*) were re-introduced into the Black Hills, South Dakota, U.S.A. in 1965. To date limited information exists concerning vital rates of this population. From 2010 to 2013, we estimated survival and cause-specific mortality of 55 adult female bighorn sheep in three herds in the east-central Black Hills. We documented 21 mortalities. Of those, pneumonia (19%) and predation (19%) accounted for most known causes of mortality; however, we were unable to ascertain cause of death for 47.6% of mortalities. We used a known fate analysis in Program MARK to estimate monthly survival; our best approximating model indicated survival differed during May–Jun compared with the remainder of the year. Monthly survival estimates for May–Jun were 0.95 (95% CI = 0.91–0.97) compared with 0.99 (95% CI = 0.98–0.99) for Jul–Apr, and overall annual survival was 0.81 (95% CI = 0.72–0.87). We found little support for the hypothesis that survival was influenced by body mass or nutritional condition (ingesta-free body fat). Our results indicated disease, predation, and other factors predisposing ewes to mortality, especially during and shortly after parturition, were contributors to the current demographic status of this population.

## INTRODUCTION

Throughout North America, bighorn sheep (*Ovis canadensis*) have declined dramatically since European settlement (Buechner, 1960) because of an array of environmental and demographic factors (Singer *et al.*, 2001; Wehausen *et al.*, 2011). Restoration efforts aimed at restoring native populations have been mixed, with many populations experiencing repeated declines and extinctions (*e.g.*, Berger, 1990). Primarily, these fluctuations have been attributed to disease (Hobbs and Miller, 1992; Cassirer and Sinclair, 2007) or predation (Kamler *et al.*, 2002; Rominger *et al.*, 2004). Pneumonia, typically *Pasturella* spp., has been particularly devastating across North America resulting in partial or complete die offs in numerous herds (*e.g.*, Cassirer *et al.*, 1996; Jorgenson *et al.*, 1997), although bighorn sheep have been documented with the pathogens and not exhibiting clinical signs (Onderka and Wishart, 1988). These die offs are often attributed to contact with domestic sheep and typically are followed by years of depressed lamb recruitment (Singer *et al.*, 2000; Monello *et al.*, 2001).

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Cougar (*Puma concolor*) predation also has been implicated as a cause of bighorn declines (Hayes *et al.*, 2000; Rominger *et al.*, 2004), with increased impacts during declines in their primary prey, mostly mule deer (*Odocoileus hemionus*; Kamler *et al.*, 2002; Rosas-Rosas *et al.*, 2003). McKinney *et al.* (2006) observed no influence of cougar abundance on predation of bighorn sheep and concluded predation may be a function of learned behavior by individuals (*e.g.*, Ross *et al.*, 1997). In addition to disease and predation, poor nutrition can predispose individuals to mortality factors, especially in temperate environments with seasonal fluctuations in abundance and quality of forage (Hobbs, 1989; Festa-Bianchet *et al.*, 1997; Monteith *et al.*, 2013). In ungulates heavier females often exhibit higher survival (Gaillard *et al.*, 2000), yet, nutritional condition (*i.e.*, percent body fat) may be more sensitive to habitat factors experienced by the individual than body mass (Monteith *et al.*, 2014). Assessing the relative contribution of extrinsic factors on patterns of survival is therefore contingent on an understanding of the nutritional limitations within a population (Monteith *et al.*, 2014).

Similar to other regions, native bighorn sheep were extirpated from the Black Hills in the early 1900's [South Dakota Department of Game, Fish and Parks (SDGF&P), 2007] and in western South Dakota around 1925 (Zimmerman, 2008). Transplants beginning in 1965 resulted in the establishment of four herds in the Black Hills region (SDGF&P, 2013). Since 2006 annual surveys conducted by SDGF&P have indicated significant declines in lamb:female ratios as well as general population declines in the east-central Black Hills. This population consisted of three subherds; Rapid Creek, Spring Creek, and Hill City, and these declines tended to coincide with an overall increase in cougar abundance. Therefore, our objectives were to estimate survival and document cause-specific mortality in adult bighorn females within these three subherds.

## METHODS

### STUDY AREA

The Black Hills are located in southwestern South Dakota and eastern Wyoming, U.S.A. Topography of the area varied from steep ridges, rock outcrops, canyonlands, and gulches to upland prairie, rolling hills, and tablelands. Elevations ranged from 973 to 2202 m above mean sea level (Froiland, 1990). Ponderosa pine (*Pinus ponderosa*) forest comprised 83% of the landscape [US Geological Survey (USGS) Gap Analysis Program, 2013]. Mixed-grass prairie (5%), riparian (4%), aspen (*Populus tremuloides*)-mixed conifer forest (3%), and developed open space (2%) were other major land-cover types present in our study area (USGS Gap Analysis Program, 2013). During our study average annual precipitation was 53 cm. Mean temperatures ranged from a maximum of 28 C in Jul to a minimum of -10 C in Jan. Climate values were based on data collected at the Hill City, South Dakota weather station from 1981–2010 [National Oceanic and Atmospheric Administration (NOAA), 2013].

Our study area was located in the east-central portion of the Black Hills (44°05' and 44°04' N latitude and 103°23' 103°27' W longitude) with bighorn sheep habitat encompassing an area of approximately 26,000 ha (Smith *et al.*, 2015). Each subherd (Rapid Creek, Spring Creek, and Hill City) maintained distinct wintering areas; however, we did observe some range overlap between Spring Creek and Rapid Creek females during the lambing season (Fig. 1). During our study no range overlap was observed between our study population and other herds in the Black Hills. In 2010 breeding-age female population estimates were: Rapid Creek = 56, Spring Creek = 50, and Hill City = 10. Estimated proportion of females radiocollared by subherd across years were: Rapid Creek 25–29% (2010–2012), Spring Creek 30–42% (2010–2012), and Hill City 90–100% (2011–2012).

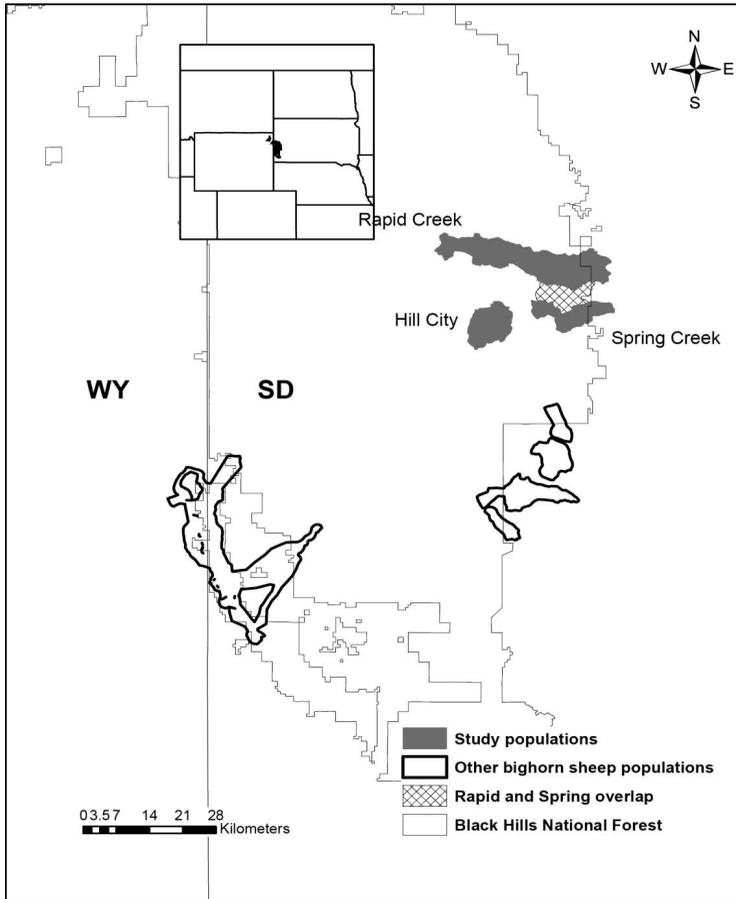


FIG. 1.—Bighorn sheep (*Ovis canadensis*) populations and locations of study populations in the Black Hills, South Dakota, U.S.A., 2010–2012

Other ungulates in the study area included mule deer, white-tailed deer (*Odocoileus virginianus*), mountain goats (*Oreamnos americanus*), and elk (*Cervus elaphus*). Mule deer tended to be the dominate ungulate in the Rapid Creek wintering area while white-tailed deer were most prevalent in the summer area and areas occupied by the Spring Creek and Hill City subherds. Cougars were considered the predominant predator of bighorn sheep in the Black Hills with populations ranging from an estimated 238 individuals in 2010 to 145 in 2013 (J. A. Jenks, South Dakota State University, Brookings, SD, pers. commun.). Other potential predators of bighorn sheep included golden eagles (*Aquila chrysaetos*), coyotes (*Canis latrans*) and bobcats (*Lynx rufus*).

#### CAPTURE AND MONITORING

We captured adult females with a drop-net baited with weed-free alfalfa hay or we chemically immobilized (BAM; 0.43 mg/kg butorphanol, 0.29 mg/kg azaperone, 0.17 mg/kg medetomidine) sheep via dart rifle (Dan-Inject, Børkop, Denmark, EU) during late-Jan to

early-Mar 2010–2012. We estimated female age class (1 y, 2 y, 3 y, or  $\geq 4$  y) based on tooth replacement (Krausman and Bowyer, 2003) and measured body mass with an electronic scale ( $\pm 1$  kg). We used ultrasonography (Aloka 210 with 5-MHz transducer, Aloka, Inc., Wallingford, CT., U.S.A.) to measure maximum depth of subcutaneous rump fat using standard methods (Cook *et al.*, 2007) and to evaluate pregnancy status (Universal Ultrasound, Bedford Hills, N.Y., U.S.A.) of captured animals. We accompanied ultrasonography with palpation based on standardized methods to estimate ingesta-free body fat (IFBFat) in other ungulate species (Cook *et al.*, 2007, 2010) but based on equations validated for bighorn sheep (T. R. Stephenson, California Department of Fish and Wildlife, Bishop, CA, pers. commun.). Pregnant females were fitted with M3930 vaginal implant transmitters (VIT) manufactured by Advanced Telemetry Systems (ATS; Isanti, MN., U.S.A.) with a redesigned wing system and antenna length of 6 cm (Bishop *et al.*, 2011). Females that were not pregnant or not checked for pregnancy at the time of capture were not fitted with VITs. Methods of VIT deployment followed Bishop *et al.* (2011). In addition to VITs, we fitted females with either very high frequency (VHF; M252OB, ATS;  $n = 50$ ) or Global Positioning System (GPS; G2110D, ATS;  $n = 12$ ) radio collars that were uniquely marked to facilitate individual identification and equipped with an 8 h mortality sensor. Over the course of the study, we replaced seven VHF radio collars with GPS collars. All procedures were approved by the South Dakota State University Animal Care and Use Committee (Approval number 09-019A) and followed recommendations of the American Society of Mammalogists (Sikes *et al.*, 2011).

We monitored females daily during the lambing season (~May–Jun) through 60 d postpartum from the ground using hand-held directional antennas (Telonics, Inc., Mesa, AZ., U.S.A.) or from a Cessna 182 (Cessna Aircraft, Co., Wichita, KS., U.S.A.) airplane. Outside of the lambing season, females were monitored 1–3 times/week using similar protocols. When we detected a mortality signal, we immediately located the collar and recorded evidence at the site of mortality to determine cause of death. When possible we collected whole carcasses of sheep for evaluation at SDGF&P (Rapid City, S.D., U.S.A.) and sent tissue samples for gross and histological examination to Washington Animal Disease Diagnostic Laboratory at Washington State University (Pullman, WA., U.S.A.). When this was not feasible, we conducted field necropsies and collected tissue for examination at Washington Animal Disease Diagnostic Laboratory. We classified mortalities as predation based on observations at the mortality site including, bite marks, caching, plucking, blood, and consumption of carcass. When cause of death could not be definitively diagnosed, we classified mortalities as unknown.

#### SURVIVAL ANALYSIS

Records from radio-tracking surveys were converted to monthly encounter histories (White and Burnham, 1999) for each year females were monitored. We censored individuals if we were unable to monitor them in a given month (*i.e.*, removed them from the at-risk group for that month) and right-censored individuals (*i.e.*, removed them from the at-risk group for the remainder of that biological year) when collars failed to transmit. Deaths were assigned to the month when date was known or mean date between the first mortality signal and the date the last active signal was obtained. To estimate survival and determine factors influencing female survival, we used the known-fate model in program MARK (White and Burnham, 1999) with the logit-link function. We used an *a priori* set of 11 candidate models to investigate the influence of temporal and individual covariates on female survival. Intrinsic variables included year, subherd, winter severity, cougar population density for the Black Hills, pregnancy status, whether females received a VIT in a given year, and three

TABLE 1.—*A priori* models constructed to determine influence of intrinsic variables on adult female bighorn sheep (*Ovis canadensis*,  $n = 55$ ) survival in the Black Hills, South Dakota, U.S.A., 2010–2012

Model	$K^a$	Description
$S_{\text{constant}}$	1	Survival was constant
$S_{\text{vit}}$	2	Survival varied by whether female was equipped with a VIT or not
$S_{\text{pregnant}}$	2	Survival varied by whether female was pregnant or not
$S_{\text{winsev}}$	2	Survival varied as a function of previous winters severity
$S_{\text{coug}}$	2	Survival varied by cougar density
$S_{\text{Season}}$	2	Survival varied between summer (May–Oct) and winter (Nov–Apr)
$S_{\text{Jun–Jul}}$	2	Survival varied during “lactation” phase
$S_{\text{May–Jun}}$	2	Survival varied during birth phase
$S_{\text{herd}}$	3	Survival varied by subherd
$S_{\text{year}}$	3	Survival varied by year
$S_t$	12	Survival varied by month

<sup>a</sup> Number of parameters

temporal models (Table 1). Because we did not have weight or IFBFat estimates for all individuals each year, we used a subset of our data and developed a second model set to evaluate the effects of weight and IFBFat on female survival (Table 2). We tested for correlation between variables using Pearson’s correlation coefficient ( $r \geq 0.71$ ) and did not include correlated variables in the same model. We tested for weight and IFBFat differences across years using an analysis of variance (SYSTAT 11.0 Systat Software Inc., Chicago, IL, U.S.A.).

We calculated winter severity by summing days with measurable snow accumulation with days that were  $\leq -7$  C based on data obtained from Hill City (for Spring Creek and Hill City subherds) and Rapid City (for Rapid Creek subherd), South Dakota weather stations from 2009–2012 [National Oceanic and Atmospheric Administration (NOAA), 2013]. Cougar population estimates were based on mark/recapture and modeling of the Black Hills cougar population (J. A. Jenks, South Dakota State University, Brookings, SD, pers. commun.). Pregnancy status of each female was determined based on ultrasound results at time of capture, or observations of females with a lamb at-heel or other visual evidence the female had given birth (*e.g.*, afterbirth present) for females that were not captured in a particular year. We also incorporated temporal models that allowed survival to vary as a function of season [winter (Nov–Apr) vs. summer (May–Oct)], and two models where survival varied across the lambing season: (1) a 2-interval model ( $S_{\text{May–Jun}}$ ) in which survival varied during May–Jun compared with the remainder of the year and (2) a 2-interval model ( $S_{\text{Jun–Jul}}$ ) in which survival varied during Jun–Jul compared with the remainder of the year (Table 1).

TABLE 2.—*A priori* models constructed to determine influence of weight and body condition (IBFat) on adult female bighorn sheep (*Ovis canadensis*,  $n = 44$ ) survival in the Black Hills, South Dakota, U.S.A., 2010–2012

Model	$K^a$	Description
$S_{\text{constant}}$	1	Survival was constant
$S_{\text{weight}}$	2	Survival varied as a function of weight
$S_{\text{IBFat}}$	2	Survival varied as a function of ingesta-free body fat
$S_{\text{weight + IBFat}}$	3	Survival varied as a function of weight plus ingesta-free body fat
$S_t$	12	Survival varied by month

<sup>a</sup> Number of parameters

TABLE 3.—Cause-specific mortality of female bighorn sheep (*Ovis canadensis*) in the Black Hills, South Dakota, 2010–2012, in relation to days since last known parturition event

ID	Subherd	Mortality date	Cause of death	Days since parturition
BH087	Hill City	5/21/2011	Infection	3
BH090	Hill City	6/7/2011	Infection	28
BH091	Spring Creek	7/17/2011	Lion	58
BH035	Spring Creek	2/27/2011	Lion	N/A
BH086	Hill City	3/24/2011	Lion	N/A
BH024	Spring Creek	5/4/2012	Lion	N/A
BH016	Spring Creek	6/20/2010	Pneumonia	29
BH080	Hill City	6/21/2012	Pneumonia	47
BH025	Spring Creek	8/17/2011	Pneumonia	92
BH027	Spring Creek	2/1/2011	Pneumonia	248
BH088	Spring Creek	5/23/2011	Unknown	5
BH067 <sup>a</sup>	Rapid Creek	5/16/2012	Unknown	17
BH020	Spring Creek	6/6/2012	Unknown	24
BH008	Rapid Creek	6/21/2012	Unknown	33
BH010	Rapid Creek	7/18/2011	Unknown	50
BH011	Rapid Creek	9/24/2010	Unknown	127
BH003	Rapid Creek	9/28/2010	Unknown	127
BH028	Spring Creek	2/4/2011	Unknown	270
BH134	Rapid Creek	4/28/2012	Unknown	N/A
BH077	Spring Creek	5/12/2012	Unknown	N/A
BH005	Rapid Creek	11/2/2010	Vehicle	163

<sup>a</sup> Three year old ewe.

We based model construction on variables we considered biologically meaningful to female bighorn sheep ecology and used Akaike's Information Criterion corrected for small sample size ( $AIC_c$ ) to select models that best described the data (Burnham and Anderson, 2002). We compared  $AIC_c$  values to select the most parsimonious model and considered models differing by  $\leq 2 \Delta AIC_c$  from the selected model as potential alternatives (Burnham and Anderson, 2002). We used Akaike's weights ( $w_i$ ) as an indication of support for each model. Because there is no current goodness-of-fit test statistic available for known fate models, we investigated model robustness by artificially inflating  $\hat{c}$  (*i.e.*, a model term representing overdispersion) from 1.0 to 3.0 (*i.e.*, no dispersion to extreme dispersion) to simulate various levels of dispersion reflected in Quasi- $AIC_c$  ( $QAIC_c$ ; Devrie *et al.*, 2003; Barber-Meyer *et al.*, 2008; Grovenburg *et al.*, 2011).

## RESULTS

We captured and radiocollared 55 adult females (three at 3 y of age; 52 at  $\geq 4$  y of age) from 2010 to 2012 (number of females lambing across years summarized in Smith *et al.*, 2014b) and documented 21 mortalities (Table 3). Percentage of ewes receiving VITs was 79% ( $n = 23$ ) in 2010, 47% ( $n = 21$ ) in 2011, and 45% ( $n = 18$ ) in 2012. In instances where we could determine cause of death, predation ( $n = 4$ ; 19.0%) and pneumonia ( $n = 4$ ; 19.0%) were the leading causes of mortality followed by infection ( $n = 2$ ; 9.5%), and vehicle ( $n = 1$ ; 4.8%); we were unable to determine ultimate cause of death for 10 (47.6%) mortalities, although we were able to conclude predation was not the ultimate cause of death as carcasses were intact. We attributed all known predation events to cougars.

TABLE 4.—Models of bighorn sheep female (*Ovis canadensis*,  $n = 55$ ) survival in the Black Hills, South Dakota, U.S.A., 2010–2012 when  $\hat{\epsilon}$  (a model term representing over dispersion) was 1.0 (*i.e.*, assumed no dispersion)

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta$ AIC <sub>c</sub> <sup>c</sup>	$w_i$ <sup>d</sup>	$K^e$	Deviance
{S <sub>May–Jun</sub> }	204.61	0.00	0.83	2	200.60
{S <sub>Season</sub> }	209.15	4.53	0.09	2	205.14
{S <sub>Jun–Jul</sub> }	211.19	6.50	0.03	2	207.11
{S <sub>constant</sub> }	212.37	7.75	0.02	1	210.36
{S <sub>vit</sub> }	213.06	8.45	0.01	2	209.05
{S <sub>pregnant</sub> }	214.20	9.58	0.01	2	210.19
{S <sub>winsev</sub> }	214.34	9.72	0.01	2	210.32
{S <sub>coug</sub> }	214.35	9.74	0.01	2	210.34
{S <sub>herd</sub> }	214.99	10.34	0.01	3	208.94
{S <sub>year</sub> }	216.05	11.43	0.00	3	210.02
{S <sub>t</sub> }	218.94	14.32	0.00	12	194.67

<sup>a</sup> Composition and description of models are listed in Table 1

<sup>b</sup> Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002)

<sup>c</sup> Difference in AIC<sub>c</sub> relative to min AIC<sub>c</sub>

<sup>d</sup> Akaike wt (Burnham and Anderson 2002)

<sup>e</sup> Number of parameters

Overall, we collected 53 unique IBFat estimates (2010 = 22, 2011 = 22, 2012 = 9) and 52 weight estimates (2010 = 21, 2011 = 22, 2012 = 9); we used an average weight value for the missing individual. Average weight of females was 70.6 kg (SE = 1.0 kg) and average IBFat was 12.7% (SE = 0.7%); they did not vary by year (weight:  $F_{2,47} = 2.371$ ,  $P = 0.104$ ; IBFat:  $F_{2,48} = 2.245$ ,  $P = 0.117$ ). Average confirmed pregnancy rate across years was 92.3% (2010 = 96.6%, 2011 = 90.0%, 2012 = 92.4%). We were unable to confirm pregnancy status of seven individuals and thus, used a 0.5 covariate value for modelling.

From our first model set assessing survival of all females, we considered model {S<sub>May–Jun</sub>} as the best approximating model ( $w_i = 0.83$ ). Remaining models were  $\geq 2$   $\Delta$ AIC<sub>c</sub> units from this model, and the weight of evidence supporting this model was  $\geq 9.6$  times greater than all other models (Table 4). Furthermore, model {S<sub>May–Jun</sub>} had the lowest QAIC<sub>c</sub> when  $\hat{\epsilon} = 2.0$  (moderate dispersion; QAIC<sub>c</sub> wt = 0.50) and through  $\hat{\epsilon} = 3.0$  (extreme dispersion; QAIC<sub>c</sub> wt = 0.30). The  $\beta$  estimate and 95% confidence intervals for May–Jun (–1.45, 95% CI = –2.32 to –0.58) indicated  $\beta \neq 0$ ; therefore, we considered survival was best explained by 2-intervals. Monthly survival estimates for May–Jun were 0.95 (95% CI = 0.91–0.97) compared to 0.99 (95% CI = 0.98–0.99) for the remaining months of the year; overall probability of surviving 12 mo was 0.81 (95% CI = 0.72–0.87). Of the 21 mortalities documented, 10 (48%) occurred in May and Jun and 11 (52%) occurred during the remainder of the year.

Survival analysis incorporating weight and IBFat indicated these variables had limited impact on overall survival (Table 5). Of the three models that incorporated these variables, all ranked below our constant model ( $w_i = 0.53$ ). Although competing models {S<sub>weight</sub>} and {S<sub>IBFat</sub>} were within 2  $\Delta$ AIC<sub>c</sub> units of the constant model,  $\beta$  estimates and 95% confidence intervals for weight ( $\beta = 0.01$ ; 95% CI = –0.03–0.04) and IBFat ( $\beta = 0.01$ ; 95% CI = –0.11–0.13) lacked support for a measurable effect ( $\beta = 0$ ). Furthermore, these models differed from the constant model by the addition of only one parameter and had

TABLE 5.—Model results of weight and body condition (IBFat) on bighorn sheep female (*Ovis canadensis*,  $n = 44$ ) survival in the Black Hills, South Dakota, U.S.A., 2010–2012 when  $\hat{\epsilon}$  (a model term representing overdispersion) was 1.0 (*i.e.*, assumed no dispersion)

Model <sup>a</sup>	AIC <sub>c</sub> <sup>b</sup>	$\Delta$ AIC <sub>c</sub> <sup>c</sup>	$w_i$ <sup>d</sup>	$K^e$	Deviance
{S <sub>constant</sub> }	110.25	0.00	0.53	1	108.24
{S <sub>weight</sub> }	112.18	1.92	0.20	2	108.15
{S <sub>IBFat</sub> }	112.25	2.00	0.20	2	108.23
{S <sub>weight + IBFat</sub> }	114.19	3.94	0.07	3	108.14
{S <sub>∅</sub> }	122.80	12.55	0.00	12	98.23

<sup>a</sup> Composition and description of models are listed in Table 2

<sup>b</sup> Akaike's Information Criterion corrected for small sample size (Burnham and Anderson 2002)

<sup>c</sup> Difference in AIC<sub>c</sub> relative to min AIC<sub>c</sub>

<sup>d</sup> Akaike wt (Burnham and Anderson 2002)

<sup>e</sup> Number of parameters

approximately the same maximized log-likelihood; therefore, we excluded these models from consideration.

## DISCUSSION

Annual survival of adult female bighorn sheep was within the range of survival rates reported elsewhere for populations not experiencing significant losses from predation (0.76–0.95%; Jorgenson *et al.*, 1997; Kamler *et al.*, 2002; Cassirer and Sinclair 2007). Although we were unable to determine the ultimate cause of death for 10 (47.6%) females, carcasses were intact and we were able to conclude predation was not the cause of death. Festa-Bianchet *et al.* (2006) documented stochastic predation episodes in three populations of bighorn sheep in Alberta that led to population declines and hypothesized these events were the result of prey specialization in cougars. Predation patterns we observed tended to be more sporadic and not indicative of prey specialization. Of the four predation events we observed, three occurred in 2011 and one in 2012. However, of the three that occurred in 2011, two were in Spring Creek and occurred 5 mo apart, while the third predation event occurred in the Hill City subherd. Nevertheless, we did observe a weak decreasing trend in annual survival correlated with predation events; 2010 exhibited the highest survival (0.83; 95% CI = 0.66–0.93) followed by 2012 (0.82; 95% CI = 0.71–0.89) and 2011 (0.78; 95% CI = 0.63–0.89), although model selection revealed little support for yearly effects.

We also failed to document any predation events in the Rapid Creek subherd and speculate this pattern may be related to the migratory nature of this subherd and the lack of spatial overlap with primary cougar habitat, especially in winter and early spring, a time when others have noted increased predation from cougars (Ross *et al.*, 1997; Hayes *et al.*, 2000; Cassirer and Sinclair, 2007). The Rapid Creek subherd generally maintained wintering grounds in a relatively open area on the west side of Rapid City and most females migrated west from 10 to 25 km to more rugged lambing grounds. These areas generally contained higher canopy cover and were more indicative of “typical” cougar habitat. However, lambing grounds were only used for part of the year, which likely decreased risk of predation for females in this herd. In contrast Spring Creek and Hill City subherds typically inhabited the same general area throughout the year, with relatively small movements occurring during the lambing season; although females with lambs in these two subherds tended to forage in more rugged areas than females without lambs or females that had lost lambs.

When compared to predation, mortality from pneumonia also seemed somewhat sporadic with one event documented in 2010 (Spring Creek) and 2012 (Hill City), and two events in

2011 (Spring Creek). While we did not detect significant differences in survival across years, Cassirer and Sinclair (2007) documented significantly lower survival in nine populations of bighorn sheep in Hells Canyon during years when pneumonia was detected. Although speculative we hypothesize several unknown mortalities were pneumonia related and may have contributed more to overall mortality. For example while we did not radiocollar adult males for our study, we observed six ram mortalities in the winter of 2010–2011 that we attributed to pneumonia based on gross examination, and Smith *et al.* (2014a) documented pneumonia as the leading cause of mortality for lambs in the Black Hills during this time. Although adult and lamb die offs from pneumonia are not necessarily linked (Cassirer and Sinclair, 2007), most mortalities were associated with whole carcasses (*i.e.*, nonpredation events) indicating pneumonia may have a greater impact on these populations than we were able to confirm.

Model selection results indicated female survival was best explained by a 2-interval model wherein survival differed during May–Jun compared to the remainder of the year. The decreased survival during this time corresponded to peak parturition for females (~15 May; Smith *et al.*, 2014), and we were able to confirm two instances of females succumbing to infection that seemed directly related to parturition. Additionally, we documented two cases of pneumonia-related mortality, one lion predation, and five mortalities from unknown causes during this time. Festa-Bianchet (1989) noted lactating females had greater fecal counts of lungworms and seemed to be less resistant to parasites and pathogens than nonlactating females. Although we were unable to quantify parasite loads, reproduction may have incurred a fitness cost during the early stages of lactation.

In temperate environments, ungulates often rely on somatic reserves to support reproduction and maintenance when forage resources cannot meet metabolic requirements (Monteith *et al.*, 2014); therefore, links between metrics of body condition and survival and reproduction are common for most species (Festa-Bianchet *et al.*, 1998; Barboza and Parker, 2008). Winter body mass and IFBFat, however, were not related to survival of adult females in our study. Furthermore, IFBFat levels we observed for bighorn sheep were markedly higher than those reported during a similar time of year for North American elk, mule deer, and moose (DelGiudice *et al.*, 2011, Cook *et al.*, 2013, Monteith *et al.*, 2014). We are unaware of other published reports for comparable IFBFat levels in bighorn sheep. Lactation is the most energetically demanding life stage for large herbivores and, therefore, can have a marked effect on seasonal fat reserves (Moen, 1978, Monteith *et al.*, 2014). Over 70% of adult females in our study were liberated from incurring such costs longer than 8 w due to high lamb mortality (Smith *et al.*, 2014). We suspect a near absence of energetic costs associated with prolonged lactation, and the low density of sheep occurring in this area as a result of decreased recruitment resulted in a population with characteristics of high nutritional condition.

Unfortunately we were unable to determine ultimate cause of death for a significant portion of female bighorn sheep in our study. Many of the carcasses were too degraded for tissue collection and on two occasions where we were able to submit samples, results were inconclusive as to ultimate cause of death. Although predation has been a significant source of mortality for both native (Holl *et al.*, 2004) and translocated-bighorn sheep (Kamler *et al.*, 2002; Rominger *et al.*, 2004), low rates of bighorn sheep in cougar diets within the Black Hills (0.6%; Smith, 2014) and all unknown mortalities lacking any evidence of predation supports our contention that predation was not the most common source of mortality for adult females during our study.

Age effects also may have contributed to our inability to determine ultimate cause of death for a number of individuals. For instance despite only collecting age class information in a systematic fashion, we did observe seven individuals with ear-tags or radiocollars from the initial release in 1991 and several other individuals that were believed to be 15+ y old (J. Kanta, South Dakota Department of Game, Fish and Parks, Rapid City, SD, pers. comm.). As survival tends to decrease with age for bighorn sheep females older than 7 y (Loison *et al.*, 1999, Festa-Bianchet *et al.*, 2003), determining ultimate cause of death would likely be more difficult if these older individuals simply succumbed to the effects of age. Our results suggest these females may still be compromised at or near parturition, and in the absence of increased recruitment or augmentation in the future, this aging population will eventually succumb to actuarial senescence.

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