



*Special Section on Mountain Sheep Management*

# Ecotypic Variation in Population Dynamics of Reintroduced Bighorn Sheep

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**ABSTRACT** Selection of bighorn sheep (*Ovis canadensis*) for translocation historically has been motivated by preservation of subspecific purity rather than by adaptation of source stocks to similar environments. Our objective was to estimate cause-specific, annual, and age-specific mortality of introduced bighorn sheep that originated at low elevations in southern British Columbia, Canada (BC ecotype), or in the Missouri River Breaks region of central Montana, USA (MT ecotype). In North Dakota, USA, mortality was similar and typically low for adult female bighorn sheep from Montana ( $0.09 \pm 0.029$  [SE]) and British Columbia ( $0.08 \pm 0.017$ ) during 2000–2016. Median life expectancy was 11 years for females that reached adulthood (2 yrs old); however, mortality accelerated with age and reached 86% by age 16. Mortalities resulted primarily from low rates of predation, disease, accidents, and unknown natural causes ( $<0.04$  [upper 90% CI]). Similar survival rates of female bighorn sheep from British Columbia and Montana, coupled with greater recruitment of bighorn sheep from Montana, resulted in a greater projected rate of increase for the MT ecotype ( $\lambda = 1.21$ ) than for the BC ecotype (1.02), and a more youthful age structure. These results support translocation of bighorn sheep from areas that are environmentally similar to areas that will be stocked. Potential benefits include more rapid population growth, greater resilience to and more rapid recovery from density-independent losses, an increased possibility that rapidly growing populations will expand into adjacent habitat, increased hunter opportunity, increased connectivity among herds, and a more complete restoration of ecosystem processes. © 2017 The Wildlife Society.

**KEY WORDS** bighorn sheep, disease, ecotype, North Dakota, *Ovis canadensis*, population growth, recruitment, restoration, survival, translocation.

Knowledge of vital rates and their population-level effects is important for identification of processes that are amenable to development of effective management strategies, whether for management of populations for harvest or for the conservation of endangered species (Cole 1957, Dinsmore and Johnson 2012). Age-specific estimates of adult survival and fecundity, which are especially valuable for long-lived species, are nevertheless rarities for ungulates in general, and for bighorn sheep (*Ovis canadensis*) in particular (Jorgenson et al. 1997). Such rarities reflect logistic difficulties of obtaining sufficiently large, well-distributed samples of known-age animals, especially for increasing or hunted populations composed primarily of young individuals. Paradoxically, population growth may be sensitive to effects of mortality even when low rates of mortality preclude estimation from achievable sample sizes. These difficulties are compounded by temporal and spatial variation, such that

short-term, small-scale studies can produce conflicting results. Accordingly, long-term studies that encompass varied ecological conditions are important for understanding ungulate population dynamics (Pierce 1999, Bleich et al. 2006).

Vital rates of bighorn sheep are of interest to biologists because adult survival and juvenile recruitment can have variable and important effects on population growth and, ultimately, on the success or failure of translocated populations. Recently, Wiedmann and Sargeant (2014) described differences in recruitment rates between sympatric bighorn sheep that originated in British Columbia (BC ecotype;  $\bar{x} = 0.24$  juveniles/adult F) and Montana (MT ecotype;  $\bar{x} = 0.56$  juveniles/adult F). The Montana ecotype comprised just 19.7% of the female population but recruited 31.6% of juvenile bighorn sheep over the long term. In contrast, the BC ecotype comprised 80.3% of the female population but recruited only 68.4% of young. Consequently, abundance of the MT ecotype increased 79.1% during their investigation, whereas the BC ecotype declined 15.7%.

Greater juvenile recruitment of the MT ecotype was associated with characteristics that could influence vulnerability to

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predation, winterkill, or disease, including greater body size and adaptation to a harsher climate (Wiedmann and Sargeant 2014). Consequently, ecotypic variation in rates or causes of mortality could potentially exacerbate or mitigate the influence of source stock on population performance in North Dakota and elsewhere. Knowledge of cause-specific mortality may also help evaluate the need, or suggest methods for, mitigation of current and future influences on populations of bighorn sheep on the eastern fringe of their geographic distribution. Our objectives were to estimate cause-specific, annual, and age-specific mortality of adult female bighorn sheep of the BC and MT ecotypes; combine estimates of mortality and recruitment to evaluate effects on population growth and composition; and discuss collective implications of recruitment, survival, selection of source stock, stochastic events, and disease for management of bighorn sheep.

## STUDY AREA

Our study area included bighorn sheep range on public and private lands primarily within exterior boundaries of the Little Missouri National Grassland (~5,000 km<sup>2</sup>; Grassland hereafter) in western North Dakota. Bighorn sheep also occupied Bureau of Land Management, National Park Service, and state lands adjacent to the Grassland. Most of the area was mixed-grass prairie dominated by needle-and-thread (*Hesperostipa comata*), western wheatgrass (*Pascopyrum smithii*), threadleaf sedge (*Carex filifolia*), and various forbs; however, dense stands of juniper (*Juniperus scopulorum*) and aspen (*Populus tremuloides*) occupied most north-facing slopes. Stringers of green ash (*Fraxinus pennsylvanicus*) were associated with draws and watercourses, and stands of cottonwood (*Populus tremuloides*) occurred in lowlands along the Little Missouri River.

The study area also was occupied by mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), and elk (*Cervus canadensis*). Mammalian and avian predators that occurred in the study area and were capable of killing bighorn sheep included mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*; Tekiel 2003, Seabloom et al. 2011). In addition to native ungulates, domestic cattle and horses were present throughout our investigation; however, domestic sheep grazing was prohibited on federal and state land within the Grassland. In May 2014, we discovered a previously unknown group of approximately 30 domestic sheep on a private inholding adjacent to bighorn sheep range within our study area. Primary land uses included grazing of domestic livestock, agriculture, and energy production. Recreational activities (hunting, biking, hiking, horseback riding, camping) also were common (Sargeant and Oehler 2007).

Elevations ranged from 637 m to 1,050 m and substrates consisted of highly erosive silts and clays, sandstone, and scoria (Bluemle 1986). The climate was semi-arid, continental, and experienced windy days frequently throughout the warm summers and cold winters. Most precipitation occurred during April–September (Jensen 1974). Precipitation records from the 5 weather stations in our study area were strongly correlated

(all  $r > 0.90$ ), as were temperature records (all  $r > 0.99$ ; Wiedmann and Bleich 2014). Monthly temperatures at Medora, North Dakota, ranged from  $-37^{\circ}\text{C}$  to  $>41^{\circ}\text{C}$  (annual  $\bar{x} = 7.43 \pm 14.76^{\circ}\text{C}$  [SD]), with average high and low temperatures during our investigation of  $30.5^{\circ}\text{C}$  and  $-17^{\circ}\text{C}$  in July and January, respectively (Western Regional Climate Center 2016). At the same station, annual precipitation ranged from 9.7 cm to 58.3 cm, with a mean of  $32.5 \pm 13.0$  cm, and long term (1948–2012) mean annual snowfall was  $82.0 \pm 13.8$  cm; during our investigation, mean annual snowfall at Medora ranged from 21 cm to 216 cm.

Interstate Highway 94 is a modern, high-speed, fenced 4-lane roadway that bisects the Grassland, and apparently has prevented contact between 11 herds (Festa-Bianchet 1986) north (~280 bighorn sheep) and 4 herds south (~50 bighorn sheep) of the roadway (Wiedmann and Hosek 2013). A single outbreak of respiratory disease having population-level implications occurred south of Interstate 94 in 1997, and was attributed to contact with domestic goats (Wiedmann and Hosek 2013). In 2008, 9 years following that outbreak, 4 females were translocated from Bullion Butte, south of Interstate 94, to Magpie Creek, north of Interstate 94.

From 1997 to 2013 no losses to respiratory disease were known to have occurred north of Interstate 94, a situation likely attributable to an absence of bighorn sheep moving northward across the highway and near absence of domestic sheep or domestic goats from bighorn sheep range north of the highway. That changed in 2014, when a sudden outbreak of respiratory disease killed 29 radio-marked bighorn sheep among 7 herds north of Interstate 94 (Wiedmann 2015).

During our investigation, the number of bighorn sheep varied from approximately 180 in 2000 (Wiedmann and Hosek 2013) to 350 in 2008 (Wiedmann 2009). Bighorn sheep were distributed among 15 herds, each of which occupied rugged terrain and associated uplands along the Little Missouri River in Billings, Dunn, Golden Valley, McKenzie, and Slope counties (Wiedmann 2016).

## METHODS

### Data Collection

We used a hand-held net-gun fired from a helicopter to capture individual bighorn sheep (Krausman et al. 1985) except in 2014, when we used a drop-net to capture bighorn sheep in Alberta, Canada. Marked bighorn sheep included individuals captured from herds throughout our study area (Wiedmann and Bleich 2014, Wiedmann and Sargeant 2014) and bighorn sheep translocated to North Dakota from Oregon, USA (2003 and 2004), Montana (2006 and 2007), and Alberta (2014). We marked captured bighorn sheep with very high frequency radio-telemetry collars equipped with mortality sensors, which we used to monitor survival from 3 November 2000 to 14 May 2016. Radio-marked individuals comprised an average of 20% of each herd (1–5 M and 2–10 F) annually.

We followed animal capture and handling guidelines established by the North Dakota Game and Fish Department, as set forth by Foster (2005) and the Animal Behavior

Society (2006), and  $\geq 1$  wildlife veterinarian was present during all translocation or collaring episodes. Prior to release, capture personnel injected each marked bighorn sheep with 3 ml of ivermectin (Ivomec<sup>TM</sup>; Merial, Duluth, GA, USA) and 3 ml of Bo-Se<sup>TM</sup> (Schering-Plough Health, Union, NJ, USA). We determined ages of females  $\leq 3$  years old by counting horn annuli; because of uncertainties associated with the use of horn annuli, we classified older females as  $\geq 4$  years old. In survival analyses, we included only animals for which we could determine age at the time of capture; we advanced age by 1 year each year of the investigation.

Throughout this investigation, we visually evaluated all bighorn sheep we encountered in the field, and those captured for translocation or collaring, for clinical evidence of respiratory disease (Wildlife Health Committee 2015). Except for animals translocated from Alberta, we examined all individuals at capture for clinical evidence of respiratory disease and tested for presence of *Brucella ovis*, *Pasteurella* spp., *Mannheimia* spp., and lungworm (*Protostrongylus* spp.) at the Caine Veterinary Teaching Center at the University of Idaho and the Veterinary Diagnostic Lab at North Dakota State University. Testing for *Mycoplasma ovipneumoniae* occurred during 2014–2016 at the Washington Animal Disease Diagnostic Lab at Washington State University. We examined bighorn sheep captured in Alberta for clinical evidence of respiratory disease and tested them for evidence of prior exposure to *B. ovis*. All available evidence, however, indicates that bighorn sheep translocated from Alberta to North Dakota in 2014 were negative for pathogens associated with respiratory disease (Appendix A).

We used a fixed-wing aircraft equipped with 2-element H antennas to locate marked bighorn sheep (Krausman et al. 1984) and determine status (i.e., alive, dead). We investigated mortality events immediately and collected biological samples (tonsillar and nasal swabs; liver, lung, heart, and spleen tissue; fecal pellets) from deceased bighorn sheep. Veterinary staff examined samples for evidence of bacterial pathogens at the Caine Veterinary Teaching Center at the University of Idaho, the North Dakota Game and Fish Department Wildlife Health Lab, the Washington Animal Disease Diagnostic Lab at Washington State University, or the Veterinary Diagnostic Lab at North Dakota State University.

We inferred disease as the cause of death from the presence of histological lesions associated with pneumonia, as illustrated by Besser et al. (2014) and laboratory confirmation of bacterial pathogens known to be associated with respiratory disease in bighorn sheep (Besser et al. 2012). We attributed deaths to predation by mountain lions based on the presence of characteristic injuries, movement and caching of carcasses, presence of sign, or other criteria described by Rominger et al. (2004). We used guidelines of Woolsey (1985) to identify predation by coyotes.

## Data Analysis

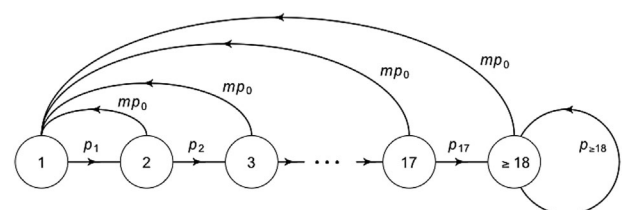
We used the approximate median date of lambing in North Dakota (15 May; Wiedmann and Hosek 2013) as the origin for age-specific and annual survival. We left-truncated

survival records at age 2 because bighorn sheep were  $>1$  year old when they were marked and because subadults ( $\leq 2$  yrs old) and adults ( $>2$  yrs old) may be differentially susceptible to various causes of mortality (Kelly 1980, Plowright et al. 2013, Manlove et al. 2016, Plowright et al. 2017). When date of death was uncertain, we used the midpoint of the interval between the last live observation and detection of death unless the extent of decomposition suggested otherwise (Bleich and Taylor 1998). We used the Kaplan–Meier method and nonparametric cumulative incidence function estimator of Heisey and Patterson (2006) to estimate age-specific survival and annual survival.

We used survival estimates with age ratios reported by Wiedmann and Sargeant (2014) to parameterize a matrix population model ( $T$ ) and explore implications of survival and fecundity for population structure, population growth, and bighorn sheep management. Our model featured 18 states, representing age classes 1 (young-of-the-yr) to  $>18$  (Fig. 1). We estimated transition probabilities ( $p_2$ – $p_{15}$ ) via local polynomial regression (loess smoothing) of annual survival versus age, extended the curve to estimate survival for ages 1 and 16–18, and applied the survival rate for 18-year-old bighorn sheep to older bighorn sheep as well. We estimated products of maternity ( $m$ ) and first-year survival ( $p_0$ ) by iteratively adjusting  $mp_0$  until lamb:female ratios matched results of Wiedmann and Sargeant (2014). We used the dominant eigenvector of  $T$  (i.e., stable age distribution) to initialize age ratios for projections. Our general approach followed methods described by Caswell (2001) and Newman et al. (2014). We used the R software language and environment (R Core Team 2016) to implement our analyses.

## RESULTS

We monitored survival of 220 adult ( $\geq 2$  yrs old) female bighorn sheep for 748 observation years (i.e., observation of 1 bighorn sheep for 1 year = 1 observation year). We documented 88 deaths. We used midpoints of intervals between observations to approximate dates of death because maximum error (median = 13 days) was negligible in the context of high daily survival rates, infrequent censoring, and our focus on annual (rather than intra-annual) rates of mortality. Kaplan–Meier estimates of annual mortality are unaffected by error in assigned dates of death unless animals



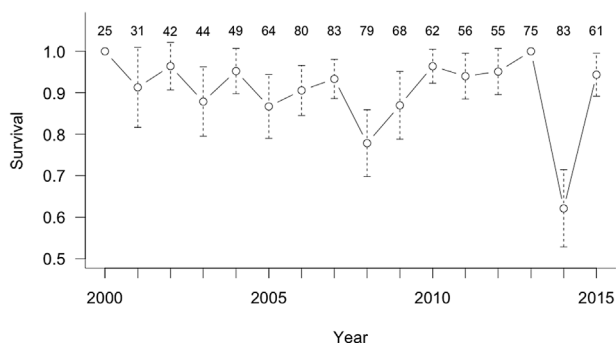
**Figure 1.** Life cycle graph depicting a matrix population model used to project growth and structure for 2 ecotypes of bighorn sheep, based on age-specific survival rates ( $p_i$ ) and ecotype-specific recruitment ( $mp_0$ ) observed in western North Dakota, USA, November 3 November 2000–14 May 2016.

are added to risk sets or censored during intervals between actual dates of death and assigned dates of death.

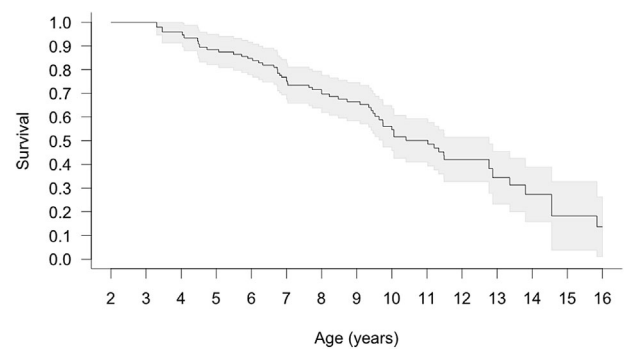
Estimates of annual survival typically exceeded 0.86; however, notable exceptions occurred in 2008 and 2014 when annual survival was 0.78 and 0.62, respectively (Fig. 2). The low survival rate in 2008 resulted from several causes of death, including predation (6 deaths), disease (3 deaths), unknown natural causes (5 deaths), and 1 fall, and was not associated with a known outbreak of disease. In contrast, low survival during 2014 resulted from an outbreak of bacterial pneumonia that caused 29 deaths of radio-marked individuals, primarily among bighorn sheep translocated from Alberta earlier that year. We excluded survival records for 2014 when calculating typical survival because we regarded the outbreak as a distinct and well-documented event of a type that warranted separate consideration.

With 2014 excluded, we documented 55 deaths among 193 bighorn sheep of known age during 638 observation years. These included 44 deaths among 144 bighorn sheep of the BC ecotype, 10 deaths among 29 bighorn sheep of the MT ecotype, and 1 death among the 24 bighorn sheep translocated from Alberta (excluded were 20 of 24 individuals that died in 2014). Average annual survival ( $0.92 \pm 0.015$  [SE]) reflected generally high and similar survival rates for bighorn sheep from the 3 different regions (i.e., BC =  $0.92 \pm 0.017$ , MT =  $0.91 \pm 0.029$ , AB =  $0.95 \pm 0.046$ ). Median survival of bighorn sheep that reached adulthood was 11 years, with approximately 86% mortality by age 16 (Fig. 3). Risk of mortality increased with age and accelerated noticeably for ages  $\geq 9$  years (Fig. 4). Whereas age-specific survival was in approximate equilibrium with mean recruitment (0.24 juveniles/adult F) of the BC ecotype (estimated  $\lambda = 1.02$ ), survival and mean recruitment (0.56 juveniles/adult F) of the MT ecotype were indicative of rapid population growth (estimated  $\lambda = 1.21$ ) and a more youthful population structure (Fig. 5).

Prominent causes of death during this investigation (Table 1) included disease, mountain lion predation, and accidents (5 falls, 1 vehicle strike, and 1 incidental capture in a leg-hold trap). Collectively, other causes (3 coyote predations, 1 illegal take, and 1 unknown cause of death)



**Figure 2.** Annual survival of adult female bighorn sheep monitored in western North Dakota, USA, November 3 November 2000–14 May 2016. Upper values denote numbers of individuals monitored. Error bars represent 90% confidence limits.

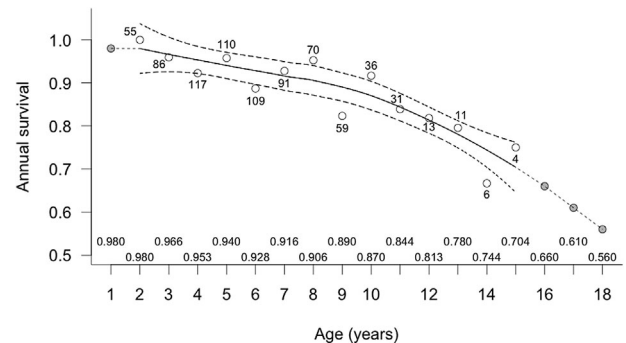


**Figure 3.** Long-term survival of adult female bighorn sheep in western North Dakota, USA, 3 November 2000–14 May 2016. The median survival time was 11 years. Shaded region denotes a 90% confidence interval.

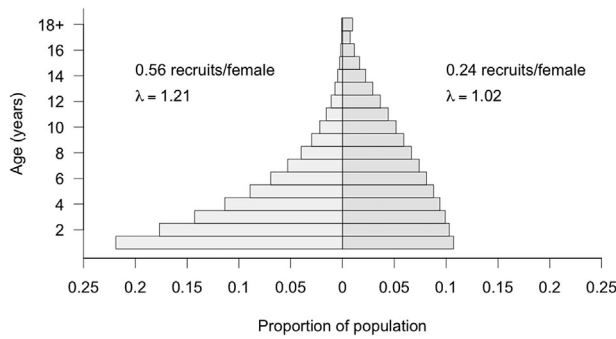
accounted for  $<1\%$  of mortality annually. At time of capture, we found no evidence of infection or exposure to bacterial pathogens most often associated with respiratory disease among those bighorn sheep translocated to North Dakota from Oregon in 2003 ( $n = 26$ ) and 2004 ( $n = 15$ ), Montana in 2006 ( $n = 19$ ) and 2007 ( $n = 20$ ), or Alberta in 2014 ( $n = 24$ ). Moreover, no disease events have been detected in any of those source populations through 2016 (N. B. MacCallum, Bighorn Wildlife Technologies; J. M. Ramsey, Montana Department of Fish, Wildlife & Parks [MFWP]; D. G. Whittaker, Oregon Department of Fish and Wildlife, personal communications). Further, evidence available before and after the translocation of bighorn sheep from Alberta to North Dakota supports our conclusion that those translocated animals were not the source of pathogens associated with the outbreak of respiratory disease in 2014 (Appendix A).

## DISCUSSION

The extirpation of bighorn sheep from much of their native range was documented by Buechner (1960). Restoration of the species in many areas has been accomplished by translocation to unoccupied historical range (Brewer et al. 2014, Wild Sheep Working Group [WSWG] 2015). More than 20,000 bighorn sheep have been translocated with



**Figure 4.** Local polynomial regression of annual survival versus age of adult female bighorn sheep in western North Dakota, USA, 3 November 2000–14 May 2016, with 90% confidence limits, numbers of individuals (adjacent to points), and fitted values (adjacent to the lower axis).



**Figure 5.** Effect of age-specific survival rates and differential recruitment on projected population growth and age structure for 2 ecotypes of bighorn sheep in western North Dakota, USA, 2000–2016. Recruitment rates for the Montana ecotype (0.56) and British Columbia ecotype (0.24) are from Wiedmann and Sargeant (2014).

mixed results in cooperative efforts to establish or augment populations in Canada and the United States (WSWG 2015). There has not been, however, a concerted effort to use translocation stock from areas most like anticipated release sites; instead, maintenance of taxonomic consistency or availability of source stock have been primary considerations in most translocations.

Potential benefits of using source stock from areas ecologically similar to those targeted for translocations are a subject of growing interest (Brewer et al. 2014, Mills 2017). Individuals inhabiting ecologically similar areas, despite being removed by distance, likely exhibit adaptations similar to target populations because they share similarities in behavior, mortality, and life-history traits (Mills 2017). For example, Kronenberger et al. (2017) demonstrated that adaptively similar, yet genetically divergent, source populations increased short-term abundance of recipient populations more than genetically similar, yet adaptively different, immigrants. Further, Buchalski et al. (2016) recommended translocations within, rather than among, the 3 lineages of desert bighorn sheep they identified as a preferred option that could conserve local adaptation, a strategy consistent with the local is best concept of Ramey (1995). As a result, use of translocation stock best adapted to a particular area, especially when combined with knowledge of recruitment rates and adult survival, likely is advantageous

**Table 1.** Estimates of annual cause-specific mortality for adult female bighorn sheep in western North Dakota, USA, 3 November 2000–14 May 2014, and 15 May 2015–14 May 2016. Excludes an epizootic outbreak of respiratory disease during 15 May 2014–14 May 2015.

Cause of death	Deaths	Mortality	SE	90% CI
Unknown natural causes <sup>a</sup>	18	0.027	0.007	0.015–0.039
Mountain lion predation	15	0.022	0.006	0.012–0.032
Disease	10	0.015	0.005	0.007–0.023
Accident	6	0.009	0.005	0.001–0.017
Other	6	0.009	0.005	0.001–0.017
Total	55	0.082	0.010	0.065–0.100

<sup>a</sup> Death did not result from traumatic injury (i.e., predation, accident, shooting, etc.).

when evaluating or mitigating anthropogenic effects on bighorn sheep on the eastern fringe of their geographic distribution in North Dakota. Among these effects are energy development (Dyke et al. 2011, Christie et al. 2015), recreational use of bighorn sheep range (Wiedmann and Bleich 2014), reestablishment and expansion of mountain lions (Wilckens et al. 2016), and an abundance of coyotes (Tucker 2015).

By the early twentieth century, native populations of bighorn sheep (then classified as *O. c. auduboni*) had been extirpated from the eastern margins of the species' range in Montana (MFWP 2010), Nebraska (Schlichtemeier 1999), North Dakota (Bailey 1926), and South Dakota (Benzon 1999). Restoration of bighorn sheep to North Dakota began in 1956 with the translocation of 18 animals from near Williams Lake, British Columbia, Canada (Knue 1991, McKenzie 1996). Subsequently, additional animals of the BC ecotype were translocated to North Dakota from British Columbia in 1989 ( $n = 10$ ) and 1996 ( $n = 20$ ), Idaho in 1990 ( $n = 23$ ) and 1991 ( $n = 38$ ), and from Oregon in 2003 ( $n = 32$ ) and 2004 ( $n = 15$ ; Wiedmann and Hosek 2013); source populations in Idaho and Oregon originally had been established by translocations from the Williams Lake region of British Columbia (Coggins et al. 1996, Oldenburg 1996) and became the progenitors of all animals considered to be California bighorn sheep (i.e., the BC ecotype) in those states. Thus, all bighorn sheep translocated to North Dakota from 1956 to 2004 had their origins in south-central British Columbia and were, at the time, classified as *O. c. californiana* (Cowan 1940); the sources were selected to maintain the presumed taxonomic integrity of bighorn sheep being reestablished in North Dakota (McKenzie and Jensen 1999).

Genetic and morphometric analyses subsequently showed that animals previously considered to be Audubon's bighorn sheep or California bighorn sheep are not distinct from the Rocky Mountain subspecies (*O. c. canadensis*). Morphological differences between the BC and MT ecotypes, which include greater body size of the MT ecotype and adaptation to harsher winter weather, exemplify ecotypic variation or genetic adaptation to local ecological conditions (Geist 1971; Wehausen and Ramey 1993, 2000). Ecotypic variation is, in part, a result of differential reproductive success and survival (van Zyll de Jong et al. 1995, Hinkes et al. 2005). Thus, demographic performance of translocated bighorn sheep is likely enhanced by selection of source stock from locations ecologically most like the proposed site of release (Whiting et al. 2012, Brewer et al. 2014) and, therefore, likely best adapted to local environmental conditions (Wehausen 1989).

Habitat and climate in Montana and elsewhere in the Rocky Mountains are more like the harsh environment of western North Dakota than the gentler terrain and milder climate of south-central British Columbia where the BC ecotype originated, an area where bighorn sheep occurred at lower elevations in drier habitats along river drainages, when compared with bighorn sheep occupying the Rocky Mountains of eastern British Columbia (Blood 1961, Sugden 1961). Although the putative subspecies have been synonymized (Wehausen and Ramey 2000), they

continue to be managed as separate ecotypes (Demarchi et al. 2000).

Motivated by the recent taxonomic revision and the historically poor population performance of the BC ecotype in North Dakota, the state began introducing bighorn sheep from Montana in 2006 (Wiedmann and Hosek 2013). Bighorn sheep of the MT ecotype are heavier, larger bodied animals and produce larger horns than bighorn sheep of the BC ecotype (Geist 1971; Boone 1988; Gilchrist 1990, 1992; Valdez and Krausman 1999); thus, they are phenotypically similar to native bighorn sheep that were extirpated from the state (Toweill and Geist 1999). Body size may have implications for survival in harsh climates (Morrison 1960, Herreid and Kessel 1967, Lindstedt and Boyce 1985, Blackburn and Hawkins 2004), such as that typical of our study area, or for defense against predators (Bleich et al. 1997, Caro 2005). Nonetheless, annual survival rates of adult females of the BC and MT ecotypes were similar and typically high in North Dakota. Dramatic ecotypic differences in population performance were thus attributable entirely to differences in recruitment (MT ecotype = 0.56 juveniles/adult F [90% CI = 0.41–0.70]; BC ecotype = 0.24 juveniles/adult F [90% CI = 0.09–0.41]; Wiedmann and Sargeant 2014). Similar adult female survival rates of both ecotypes in our investigation may have conferred a further demographic advantage to the MT ecotype, however, as Geist (1971) postulated that females most successful in rearing offspring would be expected to have lower survival rates than would less successful females (Toweill and Geist 1999). Maximizing birth and survival rates within individual subpopulations (i.e., herds) has clear benefits for the restoration of species existing in spatially structured systems (Smyser et al. 2016).

Small populations, such as those typical of bighorn sheep, are especially vulnerable to extinction (Boyce 1992). Thus, high survival rates of adult females notwithstanding (Fig. 2), ecotypic differences in population performance may have profound implications for abundance, and even persistence, of bighorn sheep in North Dakota and elsewhere. Bighorn sheep are susceptible to adult mortality from predation (Ross et al. 1997, Rominger et al. 2004) and especially periodic outbreaks of bronchopneumonia (Singer et al. 2000, Cassirer et al. 2001), such as occurred south of Interstate 94 in North Dakota in 1997 (Wiedmann and Hosek 2013) and that which began north of Interstate 94 in July 2014.

Bronchopneumonia of bighorn sheep is associated with several bacterial pathogens, including *M. ovipneumoniae*, *Mannheimia* spp., and *Bibersteinia* spp. (Cassirer et al. 2013, Dassanayake et al. 2013, Heinse et al. 2016, Wood et al. 2017). The etiology of the disease is complex and typically involves the presence of *M. ovipneumoniae* (Besser et al. 2012). Contact between domestic sheep or domestic goats and bighorn sheep is thought to be the primary mode of pathogen transmission (Besser et al. 2012, Cassirer et al. 2013). Outbreaks of respiratory disease following transmission of pathogens from domestic sheep or goats can cause extensive adult mortality, sometimes >80%. Population consequences may be further amplified by reduced survival of

offspring, an effect that can last many years (Cassirer and Sinclair 2007, Cassirer et al. 2013). Resulting periods of depressed recruitment appear to be facilitated by females that survive the initial outbreak but then transmit the pathogens to newborn young during subsequent birthing seasons (Cassirer et al. 2013). Additionally, the pathogens can be transmitted among herds by  $\geq 1$  individual moving from an infected herd to non-infected herds (O'Brien et al. 2014, Manlove et al. 2016) with landscape-level implications for conservation (Clifford et al. 2009).

Given similar adult female survival between ecotypes in this investigation, greater recruitment (Wiedmann and Sargeant 2014) would seemingly enable bighorn sheep populations to withstand increased adult mortality and recover more quickly from unanticipated losses resulting from disease. Such a benefit would be expected though, only if outbreaks do not have residual, transgenerational effects that may suppress recruitment rates for many years, as are characteristic of polymicrobial pneumonia (Cassirer et al. 2013). Logically, high recruitment rates are likely to provide larger annual increments to a population of a given size than would occur in populations of similar size but having lower recruitment rates, thereby reducing the risk of extinction for small herds. Unfortunately, recruitment (0.15 juveniles/adult F) among both ecotypes in 2016 was the lowest yet recorded in North Dakota, providing evidence for transgenerational effects such as those referenced by Cassirer et al. (2013).

Interest in bighorn sheep management is often motivated by increased opportunity for recreational hunting (Heffelfinger et al. 2013, Hurley et al. 2015, Monteith et al. 2017). However, low recruitment rates of the BC ecotype in North Dakota have supported only very limited harvest of males (Wiedmann and Hosek 2013, Wiedmann and Sargeant 2014). Recently, Monteith et al. (2017) postulated that decreasing density of female bighorn sheep on some ranges may lead to greater productivity, enhanced recruitment, larger horns among males, and increased hunter opportunity. Managing for isolation of herds via strategic harvest of females and males could also promote population stability and persistence or decrease the likelihood of the spread of chronic disease. Paradoxically, though, managing for isolation of herds via strategic harvest likely will do little to promote stability and persistence in the presence of acute outbreaks of highly contagious respiratory disease, in part because of differential habitat use between male and female bighorn sheep (Bleich et al. 1997, Rubin and Bleich 2005, Schroeder et al. 2010) or movements among herds by either sex (Bleich et al. 1996, Epps et al. 2007, Borg et al. 2017). Hence, greater rates of recruitment associated with the MT ecotype that may lead to rapid recovery from catastrophic losses, such as extreme weather events or diseases that do not persist across generations, may not be realized when populations of bighorn sheep are exposed to certain pathogens. Similarly, anticipation of robust recruitment rates characteristic of the MT ecotype, as demonstrated herein, and managing for increased hunter opportunity during an outbreak of polymicrobial pneumonia likely will not yield the desired result.

Commercial leases for grazing of domestic sheep on public lands in the United States are regulated largely by agencies within the Department of Agriculture (U.S. Forest Service) or the Department of the Interior (Bureau of Land Management). Such leases can (and have) been modified spatially or temporally and, in some cases, have been revoked, to lessen the probability of contact between domestic sheep and bighorn sheep (Schommer and Woolever 2008). Nevertheless, many private inholdings remain within tracts of federal land and are not subject to similar restrictions. Those inholdings, and private land adjacent to federal land occupied by bighorn sheep, remain problematic (U.S. Fish and Wildlife Service 2007, Clifford et al. 2009; Appendix A) in the context of disease transmission (Heinse et al. 2016) given the metapopulation structure of bighorn sheep (Schwartz et al. 1986; Bleich et al. 1990, 1996).

Collectively, recruitment and survival rates have important implications for the performance of ungulate populations (Caughley 1977). High annual survival rates among females of the BC and MT ecotypes (Figs. 3 and 4), when combined with the differences in recruitment rates between females of those ecotypes (Wiedmann and Sargeant 2014), suggest the potential for a rapid shift toward a younger age structure of bighorn sheep inhabiting North Dakota (Fig. 5). Among the potential benefits of such a strategy are greater resilience to and more rapid recovery from density-independent losses, higher rates of population growth following introductions, an increased possibility that rapidly growing populations will expand into adjacent habitat, increased hunter opportunity, increased connectivity among herds, and a more complete restoration of ecosystem processes on the eastern edge of the range of bighorn sheep. Population density and connectivity among populations have onerous implications for disease transmission (Dobson and May 1986; Simberloff and Cox 1987; Hess 1994, 1996), but with effective separation between domestic sheep and wild sheep the risk of widespread epizootics can be substantially lessened, if not eliminated (WSWG 2012).

Our results provide further support for the argument that the selection of translocation stock occupying areas most ecologically similar to planned translocation sites is an important consideration, as suggested previously by Wehausen (1989), Whiting et al. (2012), and Brewer et al. (2014). Nevertheless, adult mortality caused by pneumonia and the potential subsequent effects on recruitment we describe give cause to temper expectations despite the potential benefits associated with the use of similar ecotypes. Future chronic presence of pneumonia in North Dakota could depress population growth even if the well-adapted MT ecotype sustains an ecotypic advantage over the BC ecotype, and similar outcomes would be expected elsewhere. As a result, managers should not always anticipate potential benefits associated with the use of similar ecotypes if mitigating circumstances exist. A management strategy that emphasizes zero contact between domestic sheep and bighorn sheep, even if prior exposure has occurred (Cassirer et al. 2017), is most apt to ensure the

persistence of bighorn sheep across the landscape (WSWG 2012, Brewer et al. 2014), and there is evidence an informed public is willing to cooperate in such efforts (Heinse et al. 2016).

## MANAGEMENT IMPLICATIONS

Bighorn sheep are habitat specialists and, as such, exhibit a discontinuous distribution across their range. Further, most populations are small relative to populations of other ungulates and, thus, are especially vulnerable to extirpation. Our results document potential benefits of selecting ecotypically similar translocation stock when restoring bighorn sheep to historical ranges. Outbreaks of polymicrobial respiratory disease may diminish or negate these benefits, at least temporarily. Nevertheless, similar survival rates of adult females of the BC and MT ecotypes, when combined with substantial differences in recruitment between those ecotypes, have the potential to accelerate population recovery from density-independent losses and disease outbreaks that do not cause residual, transgenerational reductions in lamb survival. Potential benefits of using stock from source populations inhabiting systems most like proposed introduction sites likely are universal when establishing new populations or facilitating recovery of bighorn sheep populations decimated by density-independent events. Nevertheless, managers are advised that the anticipated benefits cannot be ensured in the presence of polymicrobial respiratory disease.

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## APPENDIX A. HEALTH STATUS OF ALBERTA TRANSLOCATION STOCK

Although we did not examine animals translocated from Alberta to North Dakota in 2014 for respiratory pathogens, the source population in Alberta has been characterized as productive and healthy, and has not been known to associate with domestic livestock (MacCallum 2006). Laboratory results from 1998 to 2001 indicated past exposure to *Mannheimia haemolytica* and *Pasteurella trehalosi* (MacCallum 2006), but no clinical evidence of respiratory disease has been reported. Further, 65 individuals captured at the same location and translocated to Nebraska ( $n = 45$ ) in 2012 and Nevada ( $n = 20$ ) in 2013 all tested negative for exposure to *Mannheimia* spp. and *Mycoplasma ovipneumoniae*. Additionally, 25 individuals translocated from the same Alberta location to South Dakota in 2015 were examined and no evidence of current or past exposure to either *Mannheimia* spp. or *M. ovipneumoniae* was detected. Moreover, we found no evidence of respiratory disease among 220 animals captured in North Dakota from 2000 to 2013, and no pathogens associated with respiratory disease were detected among 67 male bighorn sheep harvested by hunters during the same period. Albeit the evidence is circumstantial, these results strongly support a local source, most likely domestic sheep introduced to our study area, rather than bighorn sheep introduced from Alberta as the source of pathogens that resulted in the heavy loss of bighorn sheep during 2014.

The mean number of bighorn sheep at the capture location in Alberta each winter ( $\bar{x} = 799 \pm 82.5$  [SD]) has been substantial (MacCallum 2006, Kneteman 2016). The small number of individuals examined, however, limits the ability to reach a conclusion based on negative detection of a pathogen (Hanley and Lippman-Hand 1983, Dougherty and McInerney 2009, Ho 2009). Indeed, it is not possible to establish an unambiguous absence of pathogens associated with respiratory disease unless every individual in the population was sampled. Recognizing that, application of the method developed by Wehausen (1987) provided a high degree of confidence ( $P\bar{x} = 0.95$ ; 95% CI = 0.01) that the prevalence during each sampling period was <5%. Further, assuming that prevalence in each of the sampling periods immediately prior to (2012, 2013) or following (2015) the 2014 translocation from Alberta to North Dakota were independent, it is highly likely ( $P = 0.99$ ) that the population-wide prevalence of pathogens associated with respiratory disease during the 3 periods was <5%. Thus, it is improbable that the prevalence of pathogens associated with respiratory disease in the source population in Alberta was any different in 2014 than during 2012, 2013, or 2015.

These results are consistent with our interpretation of the low survival rate in 2014 as an unusual event that is best attributable to contact, albeit unconfirmed, between bighorn sheep and a flock of domestic sheep that was introduced to our study area. This

conclusion is further supported by the absence of clinical evidence of respiratory disease at the time of sampling in 2012, 2013, and 2015, and when animals were captured for translocation to North Dakota in 2014.

Mortalities in this investigation ascribed to undetermined natural causes (Table 1) were classified as such because they were not accompanied by evidence of trauma resulting from predation or accidents, and therefore may have been the result of disease. This uncertainty resulted because we could not always reach carcasses quickly enough for conclusive diagnosis of disease. However, we found no evidence of respiratory disease prior to 2014, the year that domestic sheep were detected on private property adjacent to bighorn sheep range in North Dakota.