2014

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Wiedmann, Brett P. and Sargeant, Glen A., "Ecotypic Variation in Recruitment of Reintroduced Bighorn Sheep: Implications for Translocation" (2014). *USGS Northern Prairie Wildlife Research Center*. 299.
http://digitalcommons.unl.edu/usgsnpwrc/299

The Journal of Wildlife Management 78(3):394–401; 2014; DOI: 10.1002/jwmg.669

*Population Ecology*

# Ecotypic Variation in Recruitment of Reintroduced Bighorn Sheep: Implications for Translocation

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**ABSTRACT** European settlement led to extirpation of native Audubon's bighorn sheep (formerly *Ovis canadensis auduboni*) from North Dakota during the early 20th century. The North Dakota Game and Fish Department subsequently introduced California bighorn sheep (formerly *O. c. californiana*) that were indigenous to the Williams Lake region of British Columbia, Canada, and Rocky Mountain bighorn sheep (*O. c. canadensis*) that were indigenous to the Sun River region of Montana. Although California bighorn sheep are no longer recognized as a distinct subspecies, they are smaller and adapted to a milder climate than either the native bighorn sheep of North Dakota or introduced bighorn sheep from Montana. Because reintroductions still play a key role in the management of bighorn sheep and because local adaptation may have substantial demographic consequences, we evaluated causes of variation in recruitment of bighorn sheep reintroduced in North Dakota. During 2006–2011, Montana stock recruited 0.54 juveniles/adult female ($n = 113$), whereas British Columbia stock recruited 0.24 juveniles/adult female ($n = 562$). Our most plausible mixed-effects logistic regression model (53% of model weight) attributed variation in recruitment to differences between source populations (odds ratio = 4.5; 90% CI = 1.5, 15.3). Greater recruitment of Montana stock (fitted mean = 0.56 juveniles/adult female; 90% CI = 0.41, 0.70) contributed to a net gain in abundance ($r = 0.15$), whereas abundance of British Columbia stock declined (fitted mean = 0.24 juveniles/adult female; 90% CI = 0.09, 0.41; $r = -0.04$). Translocations have been the primary tool used to augment and restore populations of wild sheep but often have failed to achieve objectives. Our results show that ecotypic differences among source stocks may have long-term implications for recruitment and demographic performance of reintroduced populations. Published 2014. This article is a U.S. Government work and is in the public domain in the USA.

**KEY WORDS** bighorn sheep, ecotype, North Dakota, *Ovis canadensis*, recruitment, reintroduction, translocation, wild sheep.

Many species of wildlife have declined in abundance and distribution as a result of human activity (Ceballos and Ehrlich 2002). For example, prior to European settlement of western North America, bighorn sheep (*Ovis canadensis*) ranged from Canada southward to Mexico, and from California eastward to the Dakotas and Nebraska. However, by the early 1900s, bighorn sheep were extirpated from 6 states, and only 15,000–20,000 remained in the United States and Canada (Buechner 1960, Toweill and Geist 1999).

Translocations have played a key role in restoration of bighorn sheep, which do not readily disperse and colonize vacant habitat (Geist 1971). During the past 90 years, >20,000 bighorn sheep have been translocated to restore or augment populations (Brewer et al. 2013). Although reintroductions have expanded the distribution of bighorn sheep throughout historical range, translocations often do not achieve intended results (Rowland and Schmidt 1981, Douglas and Leslie 1999). For example, Risenhoover et al. (1988) reported that the number of bighorn sheep populations in Colorado declined from 1944 to 1988, despite 27 translocations during the same period. Many reintroduced populations of bighorn sheep are at risk because they comprise few individuals and are geographically isolated (Wishart 1978, Thorne et al. 1985, Singer et al. 2000). Such populations may be less likely to persist (Berger 1990). The same is true of metapopulations numbering fewer than 150 individuals (Gilpin and Hanski 1989, Bleich et al. 1990, Fitzsimmons and Buskirk 1992).

Characteristics of source stock, habitat suitability, presence of domestic sheep, and numbers of individuals introduced are thought to affect the growth and persistence of reintroduced populations of bighorn sheep (Holl 1982, Griffith et al. 1989, Singer et al. 2000). For example, Singer et al. (2000) found that translocations of stock from native sources were twice as likely to succeed as those using descendants from reintroduced populations (i.e., dilution translocations). Toweill and Geist (1999) suggested that controlling predators, translocating younger animals, and

Received: 23 May 2013; Accepted: 10 December 2013
Published: 21 January 2014

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supplementing reintroduced populations could also improve prospects for success.

Further, wildlife populations often exhibit ecotypic variation: differences in physical characteristics or behavior that result from adaptation to local environmental conditions (Geist 1991). Such differences could potentially affect survival and reproductive success of translocated stock. Indeed, consideration of ecotypic variation is implicit in recent recommendations that bighorn sheep should be translocated from source populations that are nearest to release sites, or that have the greatest genetic or clinal similarity to extirpated populations (Ramey 1993, Fitzsimmons et al. 1997, International Union for Conservation of Nature and Natural Resources 1998, National Park Service 2006). Although wildlife managers often are limited by the availability of stock for translocation, failure to account for potential effects of ecotypic variation among source populations could potentially undermine the success of translocations (Douglas and Leslie 1999).

Management of bighorn sheep in North Dakota was constrained for decades by classification of Rocky Mountain (*O. c. canadensis*) and California bighorn sheep (formerly *O. c. californiana*) as distinct subspecies (Cowan 1940, Clark 1964). The North Dakota Game and Fish Department (NDGF) preserved the distinction by translocating only California bighorn sheep that were indigenous to the Williams Lake region of British Columbia, Canada. However, in 2005 the NDGF changed policy to permit introductions of Rocky Mountain bighorn sheep after Audubon's (formerly *O. c. auduboni*), California, and Rocky Mountain bighorn sheep were synonymized as *O. c. canadensis* (Wehausen and Ramey 1993, 2000). After reclassification, the NDGF began introducing bighorn sheep that were indigenous to the Sun River region of Montana and potentially better adapted to the harsh climate and badlands landscape of western North Dakota.

More than 1,400 translocations of wild sheep have occurred in the United States and Canada during the past 90 years (Brewer et al. 2013). In most cases, however, factors contributing to success or failure were not identified. Roy and Irby (1994) contended that more rigorous evaluations of translocations could enhance management of wild sheep. Resource selection, birth dates, and lamb survival to winter have since been compared for sympatric bighorn sheep translocated from different source populations (Kauffman et al. 2009, Whiting et al. 2011); however, ecotypic variation in recruitment has not been evaluated. We compared recruitment of translocated bighorn sheep descended from source populations in the Williams Lake region of British Columbia (BC stock) and Sun River region of Montana (MT stock). Because the native bighorn sheep of North Dakota and Montana occupied similar continental climates that were harsher than the temperate climate of southern British Columbia (Shackleton 1985, Toweill and Geist 1999), we predicted that recruitment of MT stock would exceed that of BC stock if ecotypic differences conferred an adaptive advantage in western North Dakota.

## STUDY AREA

Our study area included portions of Billings, Dunn, Golden Valley, McKenzie, and Slope counties in western North Dakota, where bighorn sheep had a discontinuous distribution in badlands habitat near the Little Missouri River. Bighorn sheep occurred on lands managed by the United States Forest Service, National Park Service, Bureau of Land Management, private landowners, and several North Dakota state agencies (Fig. 1).

Bighorn sheep were concentrated in relatively steep, rugged terrain. Elevations ranged from 637 m to 1,050 m above sea level. Substrates consisted of highly erodible silts and clays, and harder materials such as sandstone and scoria (Bluemle 1980). The climate was semi-arid, continental, and windy, with warm summers and cold winters (Jensen 1974). Temperatures during our study ranged from $-36.1^{\circ}$C to $42.2^{\circ}$C, and precipitation ranged from 24.6 cm to 36.8 cm annually (North Dakota State University 2011). Snowfall ranged from 84.1 cm to 216.4 cm annually (Desert Research Institute 2011). We calculated a winter severity index (WSI) from 1 November to 30 April during each year of our study by accumulating 1 point for each day the mean ambient temperature was $\leq -7^{\circ}$C, and an additional point for each day the snow depth was $\geq 35$ cm (Brinkman et al. 2005). Index values (92–228) were above the long-term average (199; 1950–2011) during 3 years of our 5-year study, and the WSI during 2011 was the highest on record.

Vegetation of the region was described previously by Wali et al. (1980), Jensen (1988), and Feist (1997). Primary land uses included livestock grazing, agriculture, and energy production. Recreational activities (hunting, biking, hiking, horseback riding, camping) also were common (Sargeant and Oehler 2007). In addition to bighorn sheep, our study area was occupied by cattle and horses, mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), pronghorn (*Antilocapra americana*), and elk (*Cervus elaphus*). Predators of bighorn sheep included mountain lions (*Puma concolor*), coyotes (*Canis latrans*), bobcats (*Lynx rufus*), and golden eagles (*Aquila chrysaetos*). Female bighorn sheep were not hunted during our study.

## METHODS

### Study Population

In 1956, 18 bighorn sheep (9 M, 9 F) from the Williams Lake region of British Columbia were translocated to an 80-ha enclosure in North Dakota (Murdy 1957). The captive bighorn sheep provided source stock used to repopulate vacant habitat in our study area (Knue 1991, Wiedmann 2005). Additional BC stock (31 M, 116 F) were translocated from British Columbia in 1989 and 1996, from the Owyhee River region of Idaho in 1990 and 1991, and from the John Day and Deschutes River regions of Oregon in 2003 and 2004 (Wiedmann 2005; Fig. 1). Source populations of BC stock from British Columbia, Idaho, and Oregon were genetically indistinguishable (O'Callaghan 1997). Numbers of native BC stock in British Columbia

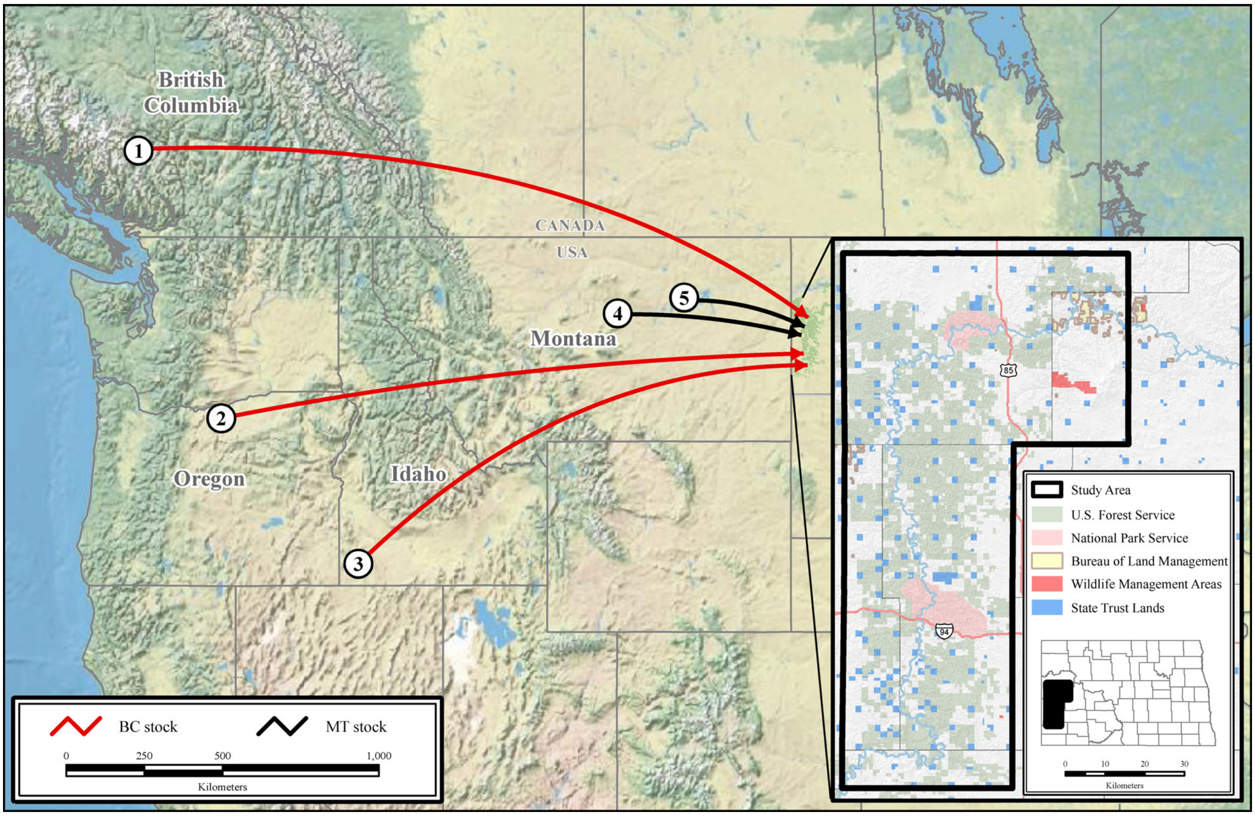

**Figure 1.** Origins of bighorn sheep translocated to historic range in North Dakota, USA (inset), during 1956–2007. British Columbia (BC) stock were obtained from 1) Williams Lake, British Columbia, Canada, 2) Owyhee River, Idaho, and 3) Deschutes and John Day Rivers, Oregon. Montana (MT) stock were obtained from 4) Upper Missouri River Breaks National Monument, Montana, and 5) Charles M. Russell National Wildlife Refuge, Montana.

increased from 1,185 in 1960 to 3,590 in 1998 despite removal of animals for translocation to 6 western states (Demarchi et al. 2000).

In 2006 and 2007, 39 bighorn sheep (8 M, 31 F) from the Missouri River Breaks region of Montana were translocated to our study area (Fig. 1). The Missouri River Breaks population was founded in 1980 with indigenous stock from the Sun River region of Montana (Montana Department of Fish, Wildlife and Parks 2010). Numbers of native bighorn sheep in the Sun River region of Montana declined slightly (−8%) from 1966 to 2008; however, contributing factors included 2 epizootics and removal of animals for translocation (Montana Department of Fish, Wildlife and Parks 2010). The mean lamb:female ratio observed during annual recruitment surveys (1982–2012) was 34:100 (Butler et al. 2013).

During 2006–2011 we deployed very high frequency (VHF) radio collars (Advanced Telemetry Systems [ATS], Isanti, MN, and Sirtrack, Havelock North, New Zealand) on 90 BC females within 14 distinct subpopulations. We fitted translocated MT stock with ATS VHF radio-collars with an attached uniquely numbered tag. We also deployed Sirtrack VHF radio collars on 33 additional BC females and 12 MT females during our study. We dosed radio-marked bighorn sheep with 3 ml of ivermectin (Ivomec$^{\text{TM}}$; Merial Limited, Duluth, GA) and 3 ml of Bo-Se$^{\text{TM}}$ (Schering-Plough Health Corporation, Union, NJ) when we captured and released them.

We conducted a census of female bighorn sheep and their offspring twice annually, during late summer and the following March 2006–2011. We used an ATS R4000 receiver and 2-element antennas (RA-2AHS, Telonics, Mesa, AZ) mounted to a fixed-wing aircraft to locate groups containing radio-marked females. Thereafter, we immediately used a handheld receiver (H.A.B.I.T. Research HR2600 Osprey, Victoria, British Columbia, Canada) and 2-element antenna (RA-2AK, Telonics) to relocate groups from the ground. We then used a 20–60× spotting scope to classify each individual as an adult male (≥2 years old), yearling male, adult female (≥2 years old), yearling female, or juvenile (Geist 1968). We used adult female:juvenile ratios observed during March censuses to estimate recruitment (Festa-Bianchet 1992).

Stock from 10 of 14 BC subpopulations did not associate with MT stock during our study. Further, MT stock translocated in 2006 were released into unoccupied habitat, and did not associate with nearby subpopulations of BC stock. Individuals from MT stock translocated in 2007 did associate with resident BC stock; however, BC and MT females occupying sympatric ranges were distinguishable because MT stock had much lighter pelage. Moreover, March censuses occurred when stocks were segregated, which was verified by identifying unique radio frequencies from females of known origin (Fig. 2).

Females from 10 of 14 BC subpopulations associated exclusively with BC males during the breeding season, and MT females translocated in 2006 were observed exclusively with MT males. Although BC and MT males did associate with females from both types where they occupied the same

**Figure 2.** Unique radio-frequencies and tag numbers were used to distinguish female bighorn sheep descended from source populations in the Williams Lake region of British Columbia, Canada, and Sun River region of Montana in North Dakota, USA, 2006–2011.

range, BC and MT stock of both sexes were segregated during the breeding season.

We followed animal capture and handling guidelines of the NDGF, as set forth by Foster (2005) and the Animal Behavior Society (2006). We conducted all captures with a hand-held net-gun fired from a helicopter (Krausman et al. 1985). Wildlife veterinarians were present during captures and while bighorn sheep were en route to release sites in North Dakota.

### Statistical Analysis

We used 6 mixed-effects logistic-regression models (Gelman and Hill 2007) to represent various hypotheses about recruitment:

Model 1 included an observation-level random effect, $\sigma_{ijk}$, representing unstructured and unexplained extrabinominal variation resulting from population influences that might have varied both geographically ($i$), annually ($k$), and between stocks ($j$). Such variation might result from local effects of disease or predation.

Model 2 included a random effect for year, $\sigma_k$, representing extrabinominal variation resulting from geographically widespread phenomena that varied annually (e.g., regional weather).

Models 3.1 and 3.2 extended models 1 and 2 by incorporating $\beta_{ij}$, which described combinations of geographic location and stock. These models provided for differences between BC and MT stock and also for geographic variation within our study area.

Models 4.1 and 4.2 extended models 1 and 2 by incorporating $\gamma_j$, a fixed effect describing the difference between the BC and MT stocks.

We used Akaike's Information Criterion, adjusted for sample size ($AIC_c$), to assess evidence for competing hypotheses represented by candidate models (Burnham and Anderson 2002). We then 1) used the "simulate" function from the R package lme4 (http://www.r-project.org/, accessed 11 Jul 2012) to generate 1,000 simulated data sets from each candidate model that was supported by our data, 2) used the "refit" function and the simulated data to generate 1,000 sets of parameter estimates for each model, 3) extracted coefficients for fixed effects, and 4) used coefficients to generate 1,000 bootstrap sets of predicted values for each model. We used standard deviations and quantiles of model-averaged predictions to estimate standard errors and 90% confidence intervals (Efron and Tibshirani 1993) that reflected both sampling variation and uncertainty associated with model selection (Burnham and Anderson 2002). We used v. 2.11 of the R language and environment (R Development Core Team 2011) and package lme4 (version 0.999375-39; Bates et al. 2011) to fit models.

## RESULTS

Our results provided greatest support for observation-level random variation and ecotypic differences in recruitment (model 4.1; 53% of model weight; Table 1). Model 4.1 estimated mean recruitment ($\hat{\rho}$) of 0.56 juveniles/adult female (90% CI = 0.41, 0.70) for MT stock and 0.24 juveniles/adult female (90% CI = 0.09, 0.41) for BC stock, for an effect size $(\Delta)\hat{\rho}$ of 0.32 juveniles/adult female (90% CI = 0.10, 0.53) and an odds ratio of 4.5 (90% CI = 1.5, 15.3).

We found no support for random annual variation in recruitment resulting from such broad-scale influences as winter weather or drought (Akaike weights = 0; models 2, 3.2, and 4.2; Table 1). However, model 3.1 (confounded effects of geographic location and origin; 33% of model weight) and, to a lesser degree, model 1 (unstructured random variation; 14% of model weight) were plausible alternatives to our top-ranked model (Table 1).

To control for confounding effects, we used a balanced subset of treatment groups (i.e., study sites occupied by both stocks) to estimate effects of origin for model 3.1 (Table 1). Recruitment estimated from model 3.1 was 0.64 juveniles/adult female (90% CI = 0.44, 0.83) for MT stock and 0.24 juveniles/adult female (90% CI = 0.10, 0.40) for BC stock, for an effect size of 0.43 juveniles/adult female (90% CI = 0.14, 0.64) and an odds ratio of 6.4 (90% CI = 1.9, 24.7).

Collectively, models 1 ($\Delta\rho = 0$), 3.1 ($\Delta\hat{\rho} = 0.43$), and 4.1 ($\Delta\hat{\rho} = 0.32$) resulted in a model-averaged effect size of 0.30 juveniles/adult female (90% CI = 0.12, 0.48) and an odds ratio of 6.2 (90% CI = 1.6, 16.2). Stock from Montana totaled 19.7% of the female population during our study, but accounted for 31.6% of the total number of lambs recruited. Taken as a whole, our results documented substantially greater recruitment by MT females than by BC females and suggested the effect was not due to differences among study sites.

Mortality of adult MT females was nearly twice that of marked BC females during 2006–2011, but greater recruit-

**Table 1.** Candidate models, corrected Akaike's Information Criterion (AIC$_c$) rankings and weights ($w_i$), estimates of recruitment (juveniles/adult female; $\hat{\rho}$), and odds ratios for bighorn sheep reintroduced in North Dakota from Montana (MT) and British Columbia (BC). Model terms include observed numbers of juveniles/adult female (p), intercepts (α), combinations of geographic location and stock (β), stock (γ), and a random effect (σ). Subscripts distinguish geographic locations ($i$), stocks ($j$), and years ($k$).

| | | | | Juveniles/adult female | | | | | Odds ratio | |
|---|---|---|---|---|---|---|---|---|---|---|
| | **Model** | **ΔAIC$_c$** | $w_i$ | $\hat{\rho}_{\mathrm{MT}}$ | **SE** | $\hat{\rho}_{\mathrm{BC}}$ | **SE** | $\hat{\sigma}$ | **MT/BC** | **90% CI** |
| 1 | $\mathrm{logit}(p_{ijk}) = \alpha + \sigma_{ijk}$ | 2.70 | 0.14 | 0.45 | 0.09 | 0.45 | 0.09 | 1.11 | | |
| 2 | $\mathrm{logit}(p_{k}) = \alpha + \sigma_{k}$ | 22.99 | 0.00 | 0.44 | 0.04 | 0.44 | 0.04 | 0 | | |
| 3.1 | $\mathrm{logit}(p_{ijk}) = \alpha + \beta_{ij} + \sigma_{ijk}$ | 0.99 | 0.33 | 0.64 | 0.12 | 0.24 | 0.09 | 0.84 | 6.4 | 1.9, 24.7 |
| 3.2 | $\mathrm{logit}(p_{ijk}) = \alpha + \beta_{ij} + \sigma_{k}$ | 10.24 | 0.00 | 0.68 | 0.08 | 0.29 | 0.06 | 0.25 | 5.4 | 2.8, 12.5 |
| 4.1 | $\mathrm{logit}(p_{ijk}) = \alpha + \gamma_{j} + \sigma_{ijk}$ | 0.00 | 0.53 | 0.56 | 0.09 | 0.24 | 0.10 | 0.90 | 4.5 | 1.5, 15.3 |
| 4.2 | $\mathrm{logit}(p_{jk}) = \alpha + \gamma_{j} + \sigma_{k}$ | 13.02 | 0.00 | 0.54 | 0.05 | 0.27 | 0.06 | 0.16 | 3.2 | 1.8, 5.8 |

ment by MT females more than compensated for those losses. Of the radio-marked BC females ($n = 53$) at the beginning of our study, 28.3% died; however, more than half (51.6%) of MT females ($N = 31$) died ($N = 14$) or dispersed ($N = 2$) during the same period. Numbers of BC stock nevertheless declined from 236 to 199 (−15.7%, $r = -0.04$) during our study, whereas numbers of MT stock increased from 43 to 77 (+79.1%, $r = 0.15$), despite greater losses of adult MT females.

## DISCUSSION

Bighorn sheep are habitat specialists (Shackleton 1985) that exhibit high fidelity to traditional home ranges (Geist 1971), which generally consist of open areas containing discontinuous patches of precipitous terrain adjacent to foraging areas (Holl 1982; Gionfriddo and Krausman 1986; Bleich et al. 1990, 1997). Knowledge of such areas is passed down to subsequent generations that typically are reluctant to pioneer and colonize vacant habitats (Geist 1971, Becker et al. 1978). Translocations of bighorn sheep have therefore played an essential role in restoration of populations to historical ranges. However, translocation of bighorn sheep is expensive, with a typical cost of approximately $1,100 per animal (Foster 2005).

Persistence of bighorn sheep is greatly influenced by population size (Geist 1975, Smith et al. 1991). For example, of the native populations studied by Berger (1990), all that comprised <50 individuals were extirpated within 50 years. In contrast, all populations comprising >100 individuals persisted for ≥70 years. Consequently, growth of restored populations to >100 individuals has been generally recognized as the benchmark for success (Singer et al. 1999). Based on this standard, only 41% of 100 translocations reviewed by Singer et al. (2000) were successful.

Low success rates, coupled with high per capita costs of capturing and transporting bighorn sheep, have greatly reduced the cost-effectiveness of translocations. Translocations also carry a biological cost in terms of impacts on source populations (Stevens and Goodson 1993), and they are not without risk to receiving populations and translocated stock (Bleich et al. 1990, Whisson et al. 2012). Factors contributing to the success or failure of reintroductions are therefore of paramount interest for management of bighorn sheep.

Northern populations of bighorn sheep formerly were classified as 3 distinct subspecies, one of which (*O. c. auduboni*) is extinct (Cowan 1940, Clark 1964). Although these distinctions were recently abandoned because molecular and morphometric variation did not meet subspecific criteria (Wehausen and Ramey 2000), they testify to substantial variation in physical characteristics of indigenous populations of bighorn sheep from different environments. Such variation within taxa is a manifestation of ecotypic variation, or genetic adaptation to local ecological conditions (Geist 1991; Wehausen and Ramey 1993, 2000).

Ecotypic variation is a result of differential reproductive success and survival (Van Zyll de Jong et al. 1995, Hinkes et al. 2005) and may have substantial implications for management (Geist 1991, Whiting et al. 2012). Prior to reclassification of *O. c. californiana* as synonymous with *O. c. canadensis* (Wehausen and Ramey 2000), agencies generally maintained the distinction between the subspecies and did not intentionally stock both into the same areas (Toweill and Geist 1999). This practice precluded observation of sympatric bighorn sheep from substantially different source populations. To our knowledge, our investigation is the first comparison of recruitment and demographic performance between sympatric bighorn sheep of different ecotypes.

Differences we observed did not mirror population performance of BC and MT stock on native range. Despite decades of intensive management by the NDGF, BC stock have consistently suffered chronically low recruitment (B. Wiedmann, unpublished data). Meanwhile, numbers of native BC stock increased dramatically in British Columbia (Demarchi et al. 2000) and numbers of native MT stock declined slightly in the Sun River region of Montana (Montana Department of Fish, Wildlife and Parks 2010). In contrast, abundance of BC stock declined 16% and MT stock increased 79% during our study. Our results therefore suggest that potential demographic performance of reintroduced bighorn sheep may be enhanced by selection of source stock adapted to similar environments. For example, the largest-bodied bighorn sheep in North America are generally found at the northern portions of their range or at high elevations, under conditions similar to those experienced in North Dakota: high-quality summer forage is abundant and winters are typically severe (Geist 1971, Blackburn et al. 1999). Larger ecotypes typically give birth to larger lambs that are more capable of surviving inclement weather during the birthing season and subsequent first winter of life (Shackleton et al. 1999, Toweill and Geist 1999). The superior demographic performance of MT stock in North Dakota likely reflects an advantage conferred by larger body size in both environments.

Bighorn sheep translocated to our study area from Montana were relatively young (median = 4 years old, $N = 31$). However, the longevity of bighorn sheep and late onset of reproductive senescence limited the potential for contribution to effects we observed. For example, Bérubé et al. (1999) observed age-related decreases in survival 6–7 years before decreases in recruitment, and long-lived females sustained high reproductive success throughout their lifetime. Moreover, birth rates were <0.20 for 2-year-old females and increased until 5–6 years of age, when they exceeded 0.9. Such age-related variation in survival and reproduction would have dampened, rather than produced, differences in recruitment rates of BC and MT stock.

Although origins of stock for translocation may substantially affect demographic performance, other factors also commonly prevent wild sheep populations from achieving their full potential. For example, diseases (Gross et al. 2000, Cassirer et al. 2013), predation (Kamler et al. 2002, Rominger et al. 2004), and possibly low genetic diversity resulting from inbreeding within small founder groups (Hogg et al. 2006, Foster and Whittaker 2010) may all stifle demographic performance of reintroduced populations. Whether timing of parturition of source stock is synchronized with the availability of nutritious forage during the lambing season may also be an important consideration (Whiting et al. 2011, 2012).

Effects of other influences should magnify, rather than diminish, interest in ecotypic variation because demographic advantages of locally adapted bighorn sheep may compensate and allow introduced populations to persist, or even increase, under conditions that might otherwise cause translocations to fail (Rominger et al. 2004). For example, newly introduced MT females achieved greater recruitment and population growth than BC stock despite greater levels of adult mortality caused primarily by cougar predation and vehicle collisions in the study area (B. Wiedmann, unpublished data). In contrast, abundance of BC stock declined during the same period despite much lower levels of adult mortality than bighorn sheep introduced from MT.

Although adaptation to similar environments may be an important consideration for selection of source stocks, it may not be entirely sufficient; behavioral adaptation also may be critical and has not always been given adequate consideration (Hutchins and Geist 1987, Warren et al. 1996, Frair et al. 2007). Neglecting the adaptive idiosyncrasies of mountain ungulates in management decisions may result in failure of translocations because introduced animals that lack site-specific knowledge of foraging areas, water sources, bedding areas, mineral licks, and suitable lambing habitat may be at a disadvantage (Geist 1975, Risenhoover et al. 1988, Bleich et al. 1997, Douglas and Leslie 1999, Scillitani et al. 2013). Further, bighorn sheep from migratory populations that are adapted to high-elevation, alpine habitats may not acclimate adequately to low-elevation habitats that are typically drier and more suited to non-migratory behavior, or vice-versa (Easterly 2009).

Adaptations of taxa to local environments can substantially affect behavior and demography of populations (Åbjörnsson et al. 2004, Whiting et al. 2012), particularly as they relate to wild sheep, where female offspring typically adopt their natal home ranges (Geist 1971). However, if reintroduced populations of bighorn sheep realize short-term adaptations to dissimilar habitats, it was not evident during our study. Indeed, BC stock occupied our study area 5 decades prior to the introduction of MT stock but realized substantially lower recruitment and population growth than MT stock, and the disparity was greatest where both occupied the same range.

Although initial translocations (1958–1961) of bighorn sheep from a captive source were largely ineffective, the Missouri River Breaks population in Montana thrived after 1980, when 56 animals were translocated from the Sun River region of that state (Sullivan et al. 1998). The translocated stock soon colonized most of the Breaks region and not only provided 149 animals for translocations, but increased to >1,000 individuals by 2008 (Montana Department of Fish, Wildlife and Parks 2010). Not surprisingly, bighorn sheep translocated from the Missouri River Breaks region of Montana to the ecologically similar Little Missouri River region of North Dakota achieved similar rates of population growth. In contrast, BC stock have fared poorly in North Dakota but have thrived in milder regions of Idaho, Nevada, Oregon, Utah, and Washington (Toweill and Geist 1999).

## MANAGEMENT IMPLICATIONS

Translocations are likely to be an important management tool in the continued recovery and persistence of bighorn sheep (Larkins 2010). Because wild sheep are widely distributed and exhibit local adaptations to clinal discontinuity throughout their global range (Clark 1964, Mitchell and Frisina 2007), translocations may also become an increasingly important tool used internationally for the conservation and management of declining populations of wild sheep throughout Europe and Asia (Kence et al. 2002, Maroney and Paltsyn 2003). Our results suggest that consideration of ecotypic variation among sources of translocation stock can greatly improve prospects for successful reintroductions of mountain sheep.

## ACKNOWLEDGMENTS

We thank the North Dakota Game and Fish Department, Wild Sheep Foundation–Midwest Chapter, the U.S. Geological Survey Northern Prairie Wildlife Research Center, and the Bureau of Land Management—North Dakota Field Office for funding this project. We thank the British Columbia Ministry of Environment, Idaho Fish and Game Department, Montana Department of Fish, Wildlife and Parks, and Oregon Department of Fish and Wildlife for their generosity in supplying translocation stock to North Dakota. We thank W. Jensen for computing winter severity indices; B. Hosek, R. Johnson, J. Kolar, S. Richardson, B. Stillings, and W. Tidball for their technical assistance; and pilots B. Berentson, J. Faught, J. Rubbert, and M. Shelton for assisting with capture operations and radio-tracking. We are grateful to V. Bleich, M. Festa-Bianchet, K. Hurley, M. Sullivan, and 1 anonymous reviewer for providing comments that improved early drafts of this manuscript. Any use of trade, firm, or product names is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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