



## Policy analysis

## Range-wide monitoring of population trends for Rocky Mountain bighorn sheep



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## ABSTRACT

Species conservation requires monitoring and management that extends beyond the local population, yet studies evaluating population trends and management outcomes across the spatial range of a species remain rare. We conducted the first range-wide assessment of population trends for the iconic Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) of North America to investigate links between population trends and translocation history. Millions of US dollars have been spent translocating bighorn sheep to achieve conservation objectives, yet a range-wide assessment is lacking. We collected bighorn sheep population estimates for 217 populations across ten US states and two Canadian provinces. We categorized each population by translocation status: native (populations received no translocations), augmented (native populations supplemented with translocation), or reintroduced (populations beginning from translocation). Fifty-eight percent of populations increased in recent years. While most reintroduced and native populations increased in the last 5 years of records, almost double the number of augmented populations declined compared to increased. Reintroduced and augmented populations from the north-central portion of bighorn sheep range declined the most in the last 5 years of records, while southern populations tended to be more stable. Although Rocky Mountain bighorn sheep appear to be a conservation and restoration success, the threat of local population loss remains high in certain regions. We show how amalgamating multi-jurisdictional population data can assist in determining wildlife status and assessing broad-scale management outcomes.

## 1. Introduction

Globally, species conservation requires monitoring and management that extends beyond a local population (Baillie et al., 2000; Collen et al., 2011; May, 1994), yet there remains a crucial gap between how patterns and processes in a local population scale up to the species level (Collen et al., 2011; Noon et al., 2012). For wide-ranging species, direct species assessments typically consist of local population estimates and management outcomes considered in isolation (Clapp and Beck, 2016; Stephen et al., 2005; Weilenmann et al., 2011). For many species of conservation concern, funding limitations and time constraints mean agencies managing large landscapes often use coarse filter approaches to conduct indirect assessments, like managing vegetation communities to infer changes in the status of species (Noon et al., 2012, 2009;

Schlossberg and King, 2009). While individual population assessments can effectively gauge the outcomes of management in a single location, they do not provide the information necessary to optimize conservation efforts across a broader range (May, 1994). Literature reviews and meta-analyses provide additional insights; however, differences in methodology and definitions of 'success' often limit clear, holistic inference from these studies (Cook et al., 2014; Fischer and Lindenmayer, 2000; Lajeunesse and Forbes, 2003). This can result in limited conservation funds being used for costly management tactics without a full understanding of their value for species-wide conservation.

Globally, conservation practitioners have used translocation, the intentional movement of living organisms from one location to another (IUCN, 1987), as a tactic to supplement the more traditional strategy of direct species and habitat protection when the latter are unable to

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prevent declines in populations (Ewen et al., 2011; Griffith et al., 1989). Many taxa have been translocated over the last century in efforts to boost population growth and genetic diversity within threatened populations, reintroduce extirpated populations, and introduce animals to uninhabited ranges (Seddon, 2010). Organization of translocation efforts can require cooperation across multiple jurisdictions (e.g., Wild Sheep Working Group, 2015). However, the impacts of translocation on population growth tend to be monitored locally (Brichieri-Colombi and Moehrenschlager, 2016; Rominger et al., 2004). Reviews of translocation efforts indicate mixed success (Brichieri-Colombi and Moehrenschlager, 2016; Fischer and Lindenmayer, 2000). Translocation projects can cost upwards of tens of thousands of US Dollars (Bangs and Fritts, 1996; Fischer and Lindenmayer, 2000; Weise et al., 2014). Understanding species-level translocation impacts is becoming more important, as the use of translocation is projected to increase in the future (Swan et al., 2018).

Intensive population monitoring efforts for many species in recent decades have created extensive data on individual populations across different jurisdictions. While an assessment conducted for a single population may not provide the information necessary for species-level conservation, a spatially extensive collection of population time-series data can provide the information necessary to assess species-level risk (Collen et al., 2009; Loh et al., 2005). The loss of local populations can be an indicator of species-level extinction risk (Ceballos and Ehrlich, 2002; Collen et al., 2011, 2009). Moreover, when management tactics like translocation are widespread across a species range, amalgamating individual population monitoring data can be more fruitful for the assessment of management outcomes at a species-level. Unfortunately, such studies are rare given logistical difficulties of compiling datasets from many individuals and organizations involved in collecting such data across the species' range.

Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) are an iconic game species that have been a conservation priority in North America for the last century (Krausman, 2000). Following European settlement of the West, Rocky Mountain bighorn sheep numbers decreased from an estimated ~2 million to < 42,000 in the 1970s (Buechner, 1960; Schmidt and Gilbert, 1978). Translocation and re-introduction has been a primary management tool for re-establishing extirpated populations and increasing numbers in declining populations across bighorn sheep range. Over 21,500 bighorn sheep have been translocated in almost 1500 translocation projects across the United States and Canada over the last century (Wild Sheep Working Group, 2015). Although guidelines and monitoring protocols have been developed and reviewed to improve the outcomes of bighorn sheep translocation (Cassirer et al., 2018; Poirier and Festa-Bianchet, 2018; Singer et al., 2000a), neither broad-scale population trends nor the impacts of translocation on population trends across North America have been assessed. This can likely be attributed to a previous deficiency of spatially extensive and long-term population data for Rocky Mountain bighorn sheep. Assessments of population trends tend to be restricted to a few populations (e.g., Festa-Bianchet et al., 2006) or a state (e.g., MFWP, 2009). Such assessments can be difficult to compare across broader regions because of differences in study design and modelling approaches. Singer et al. (2000b) summarized re-introduction success rates of 100 populations of Rocky Mountain and Desert bighorn sheep (*O. c. nelsoni*) in southwestern USA, demonstrating only a 30% success rate in introduction attempts. How these trends compare with other regions within bighorn range is unclear. Moreover, how trends in re-introduced populations contrast with those in native populations that have or have not been augmented with translocated sheep remains unknown. However, increasingly extensive monitoring efforts by federal, state, and provincial agencies in both the United States and Canada has progressively collected more thorough population data (e.g., George et al., 2009; MFWP, 2009), making such comparisons ever more feasible.

We conducted the first continental, range-wide assessment of

population trends for the iconic Rocky Mountain bighorn sheep of North America to investigate links between population trends and population translocation status. We surveyed state and provincial natural resource agency staff and reports and the scientific literature to compile annual population counts and estimates for 217 populations of Rocky Mountain bighorn sheep across the United States and Canada that differed with respect to translocation occurrence, and whether they had been used to re-populate extirpated populations or supplement existing populations. These data were used to (1) provide a first look at the most recent status of Rocky Mountain bighorn sheep populations across their range and (2) estimate patterns in recent population trends among native, augmented, and reintroduced populations of Rocky Mountain bighorn sheep. Our findings will help with the conservation and management of bighorn sheep across their range.

## 2. Materials and methods

### 2.1. Data collection and sorting

We collected population counts and estimates of Rocky Mountain bighorn sheep over the last century from government reports published during or before 2017 for Alberta, British Columbia, Colorado, Idaho, Montana, New Mexico, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming (Appendix A). We supplemented these reports with survey responses that we received from wildlife managers in Wyoming and Montana (Appendix B), primary literature searches, and telephone calls to bighorn sheep managers in North Dakota and South Dakota (Appendix A). States and provinces were only included in our study if we were able to collect adequate data for model convergence (i.e., a sufficiently large sample size for at least one population) from public records.

We collected population counts and estimates of Rocky Mountain bighorn sheep, population type (reintroduced, augmented, or native), introduction and augmentation dates and numbers, population removals, population survey methods, and population range information for populations classified as the Rocky Mountain subspecies. Reintroduced populations were designated as populations that originated from a translocation. Reintroduced populations may have experienced more than one translocation effort (e.g., Clapp et al., 2014). Augmented populations were native herds augmented with translocated individuals. We considered native populations those without any augmentation through translocation. We recorded all populations where we identified at least four counts or estimates that spanned at least 5 years (the minimum sample size where models were able to converge). Populations that resulted from spread from adjacent populations (pioneering populations) were not included in our assessment. This resulted in 217 populations with sufficient information to include in our analyses (Table 1; Appendix C). Different states and provinces defined populations differently. Thus, we compared trends through time among populations, but did not compare population size.

### 2.2. Analysis

To assess overall population trends in bighorn sheep, we fit a discrete Gompertz model (Gompertz, 1825) to population counts or estimates for each population. Because our objective was to compare population trends across Rocky Mountain bighorn sheep range, we chose to maximize the generality of model outputs across populations by selecting a single model (i.e., the Gompertz model) to model population dynamics rather than conducting model selection across a range of models to determine best fit for each individual population (Levins, 1966). The Gompertz model traditionally incorporates density dependence ( $d$ ), which has been shown to be an important parameter in some previous population analyses of bighorn sheep (e.g., Colchero et al., 2009). However, density dependence does not always emerge in bighorn sheep population dynamics (e.g., White et al., 2008; Wang et al.,

2008). Thus, we followed the approach of Koons et al. (2015), which allowed us to consider the potential for negative density dependence, density independence (no density dependence), and positive density dependence (Koons et al., 2015; Wang et al., 2008). See Appendix D for a description of our use of the Gompertz model including all model equations.

We estimated parameters using Bayesian state-space modelling. The posterior distributions of estimated parameters were estimated using Markov Chain Monte Carlo computation in JAGS (Plummer, 2003) using R2Jags (Su and Yajima, 2015) in the R statistical computing environment (R Core Team, 2017). Population models were not interpreted, and parameter estimates not reported or included in further analyses if Gelman's R statistic showed poor convergence. In addition, we did not model populations that had been extirpated (reached zero individuals without subsequent successful translocations over the period of recorded data). This resulted in 199 populations that were successfully modelled (Appendices E, F). We used a 75% credible interval for estimated parameters because it provided more descriptive information about posterior distributions than more classically chosen cut-off values like 95% used in frequentist statistics. A full description of modelling methods including prior specification can be found in the Appendix D.

The length of time series data varied by population (from 5 to 90 years; Appendix C). Model coefficients based on up to 90 years of time series data may not represent the most comparable, most recent, and relevant trends. Thus, we also used the last 5 years of model estimates for each population to characterize the most recently documented population dynamics over an equal time interval across populations. To assess proportional changes through time across populations, we calculated the percent change between the last recorded population estimate and the population estimate 5 years prior to that estimate. For all populations, the average start year for this calculation was  $2008 \pm 3$  SD (range of 1995–2012).

We created 3 linear models to determine the relationship between (1) percent change estimates for the last 5 years of records, (2) density dependence ( $d$ ), and (3) intrinsic rates of increase ( $r$ ; dependent variables) and translocation status (independent variable) of populations. The dependent variables, density dependence and intrinsic rate of increase, were the coefficients generated from each population's Bayesian state space model. The percent change dependent variable represented the proportional difference between the last recorded population estimate and the population estimate 5 years prior to that estimate for each population. We included latitude, longitude, the length of a population data set in years, and the number of population estimates recorded for each population as covariates in all models. We used Moran's  $I$  to test for spatial autocorrelation among populations (using approximate

**Table 1**

The data range in years and number of reintroduced, augmented, and native populations of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) collected across the western United States and Canada for this study.

State	Data range in years	Number of populations			
		Total	Reintroduced	Augmented	Native
Alberta	1971–2015	10	0	3	7
British Columbia	1927–2017	13	1	5	7
Colorado	1944–2015	77	40	23	14
Idaho	1920–2010	12	6	3	3
Montana	1939–2016	45	21	6	18
New Mexico	1964–2014	6	6	0	0
North Dakota	1956–2015	9	9	0	0
Oregon	1971–2014	8	8	0	0
South Dakota	1922–2014	3	3	0	0
Utah	1952–2014	15	15	0	0
Washington	1957–2016	10	10	0	0
Wyoming	1958–2015	9	5	0	4
TOTAL		217	124	40	53

latitude and longitude of the population location) for intrinsic rate of increase, density dependence, and percent change in the last 5 years of records (Paradis and Schliep, 2018). Where Moran's  $I$  indicated that spatial autocorrelation was present, we used approximate location of populations to calculate a distance matrix for populations using Euclidian distances (Oksanen et al., 2019), following guidelines from Legendre (1993). We extracted the eigenvectors of neighbor matrices (PCNM; Borcard et al., 2004; Borcard and Legendre, 2002; Dray et al., 2006) associated with the distance matrix to approximate the spatial structure of the data. We added these as independent variables to the linear models for autocorrelated variables. This accounts for spatial autocorrelation in the data at the spatial scales identified by the PCNM analysis (Borcard et al., 1992). All analyses were conducted using R statistical software (R Core Team, 2017).

The Wasatch Mountains Timpanogos population in Utah represented an outlier in the data for 'intrinsic rates of increase' that violated linear model assumptions. When we removed this population from the data set, it had a stark influence on the significance of 'the length of a population data set' in our linear model estimates. This population represented a small data set (4 population estimates recorded over 9 years) with the highest recorded intrinsic rate of increase (4-times larger than the next highest modelled value). Based on this, and the modelled relationship that emerged between 'the length of a population data set' and 'intrinsic rate of increase,' we removed this population from our model. Further discussion of this outlier can be found in Appendix G.

We used the Getis-Ord  $Gi^*$  statistic (Getis and Ord, 1992; Ord and Getis, 1995), calculated with ArcGIS v.10.4.1, to identify local patterning in intrinsic rate of increase, density dependence, and percent change in the last 5 years of records. The z-score and associated p-value calculated for each population indicated the level of spatial clustering of high and low values. Maps were generated to locate regions of spatial clustering across bighorn sheep range (Appendix H). A more detailed description of the calculation of the Getis-Ord  $Gi^*$  statistic can be found in the Appendix H.

### 3. Results

#### 3.1. Species status

Intrinsic rates of increase were overwhelmingly positive across the populations we studied, with 95% of populations having a positive intrinsic rate of increase when all available data were analyzed (Fig. 1; Appendix E). Average intrinsic rate of increase across populations was  $0.010 \pm 0.001$  SE. However, there were high levels of uncertainty, with only 4% of populations having a 75% credible interval that did not encompass zero (Fig. 1; Appendix E). There were no strong patterns in intrinsic rates of increase related to the jurisdiction a population fell in nor tied to latitude or longitude (Fig. 1; Table 2; Appendix H). Moran's  $I$  tests indicated no spatial autocorrelation among populations for intrinsic rate of increase (Table 2). However, intrinsic rate of increase was significantly influenced by the length of data records, where longer data records had larger intrinsic rates of increase (Table 3; but see discussion in Appendix G).

Density dependence was low, averaging  $-0.003 \pm 0.002$  SE across populations in Rocky Mountain bighorn range (Fig. 1). Thirty-seven percent of populations had  $d$  values with a 75% credible interval that did not encompass zero (Appendix E). Populations tended to display stronger negative density dependence (increasing population density correlates with decreasing growth rates) than positive (increasing population density correlates with increasing growth rates; Appendix E). The average density dependence value across populations displaying signs of positive density dependence was  $0.007 \pm 0.002$  SE, while the average density dependence value of populations displaying signs of negative density dependence was  $-0.013 \pm 0.002$  SE. There were no strong latitudinal or longitudinal patterns in density dependence

(Fig. 1; Table 3). Unlike with intrinsic rates of increase, there was no influence of data length on density dependence (Table 3). Moran's *I* tests indicated no spatial autocorrelation among populations for density dependence (Table 2).

Across bighorn sheep range, the average percent change in the last 5 years of records for bighorn sheep populations was  $6.7\% \pm 3.1$  SE. Of the populations assessed, 58% had a positive percent change in the last 5 years of records in contrast with 42% that had declined (Table 4). The average percent change in declining populations ( $-26.9\% \pm 2.54$  SE) was similar to that of increasing populations ( $31.3\% \pm 3.7$ ; Table 4). The greatest percent declines and increases in populations in the last 5 years of records were concentrated in north-central regions of bighorn sheep range (average start year of calculation was  $2006 \pm 3$  SD), while populations were more stable in southern regions (average start year for calculation was  $2009 \pm 3$  SD; Fig. 2; Appendix H). There was spatial autocorrelation in percent change in the last 5 years of records among populations (Table 2). We included PCNMs in the linear model to approximate the autocorrelation structure so that parameter estimates would not be biased. We removed latitude and longitude from our model due to high correlation with PCNMs (Pearson Correlation Coefficients of 0.93 and 0.97). There was no influence of data length on percent change in the last 5 years of records (Table 3).

### 3.2. Translocation status

Of the 199 populations modelled, 53.7% were reintroduced, 26.6% were native, and 19.6% were augmented. Translocation status was a significant predictor of intrinsic rate of increase (Table 3). Reintroduced populations had significantly higher estimated intrinsic rates of increase than augmented and native populations (Table 3). Only reintroduced populations had a 75% credible interval not encompassing zero (Appendix E). In contrast, the strongest density dependent population growth emerged in native populations (Table 5). Native populations had significantly stronger negative density dependence than reintroduced populations; however, there were no other strong differences in density dependence based on translocation status (Table 3).

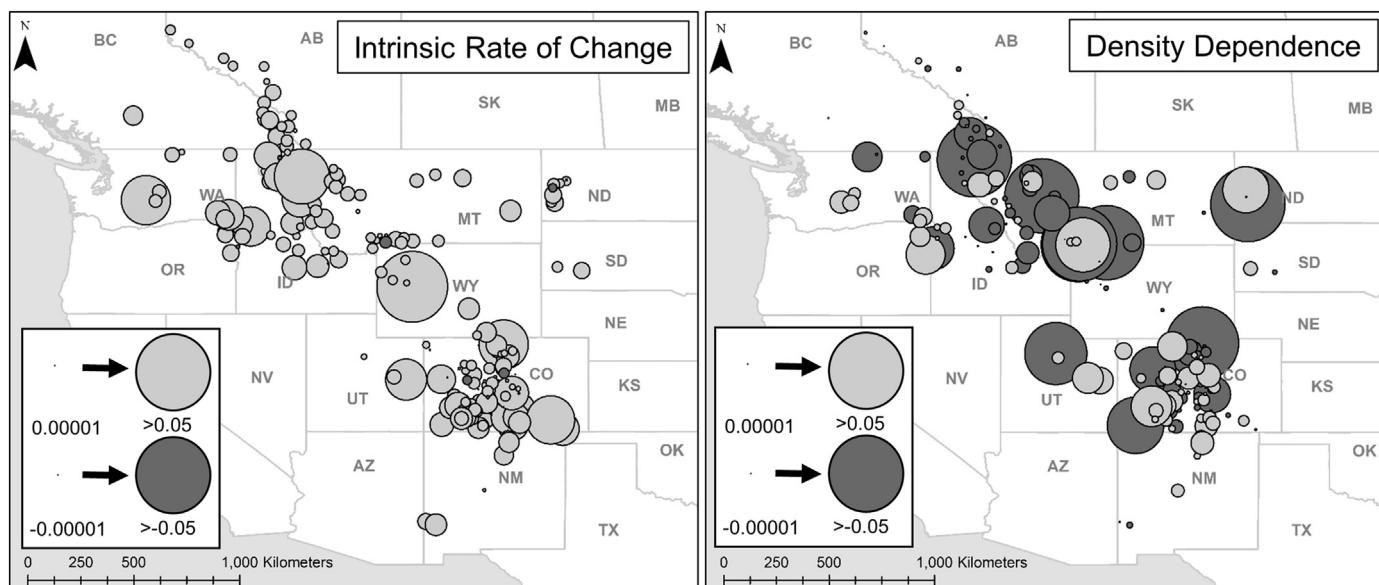
Most reintroduced and native populations increased in the last 5 years of records (68 populations increasing compared to 39 decreasing; 32 populations increasing compared to 21 decreasing, respectively), while almost double the number of augmented populations

had declined compared to increased (Table 4). Native populations had significantly greater percent change in the last 5 years of records compared to both augmented and reintroduced populations. Of those populations that increased, native populations increased by  $42.5\% \pm 9.6$  SE, reintroduced populations increased by  $30.1\% \pm 4.2$  SE, and augmented populations increased by  $12.8\% \pm 2.1$  SE on average (Table 4; Fig. 2). In both reintroduced and augmented populations, the greatest declines in the last 5 years of records occurred in the north-central region of bighorn range (Fig. 2; Appendix H). In native populations, there were no strong spatial patterns tied to percent change in the last 5 years of records (Fig. 2; Appendix H).

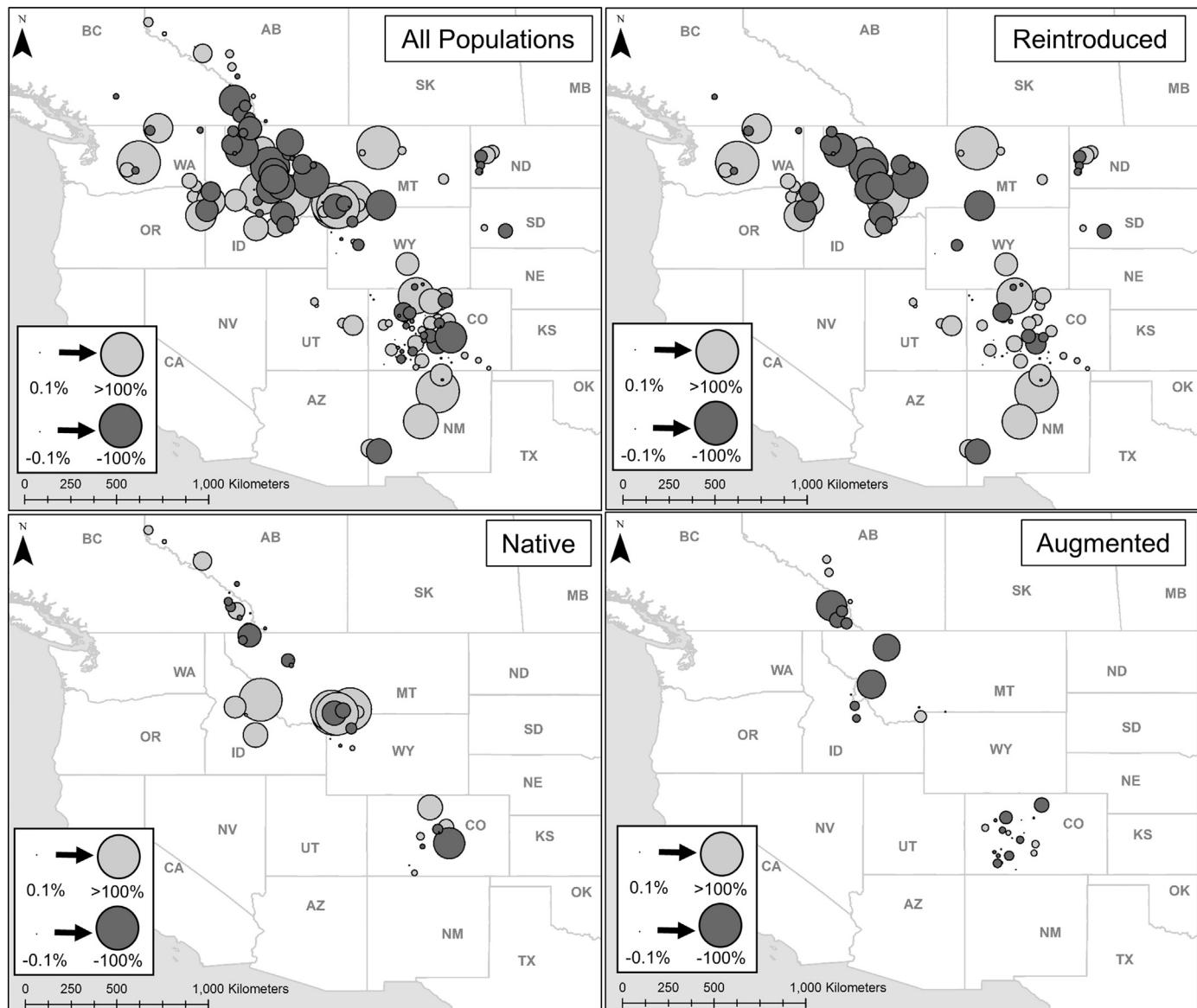
Patterns in percent change in the last 5 years of records varied across jurisdictional boundaries and population translocation status. Across populations, the average percent change in the last 5 years of records of increasing populations exceeded that of decreasing populations (Table 4; Fig. 2). However, the average percent decrease in the last 5 years of records in augmented populations was nearly double that of the average percent increase (Table 4; Fig. 2). This same pattern was apparent for reintroduced populations in Idaho and South Dakota (Table 4). Similarly, while most reintroduced and native populations were increasing across bighorn range, in Montana, 57% of reintroduced populations declined in the last 5 years of records (Table 4; Fig. 2). In Alberta and British Columbia, there were a greater number of native populations in decline than increasing in the last 5 years of records (Table 4). Similarly, augmented populations were generally in decline across bighorn sheep range, however, all of Alberta's augmented populations increased in the last 5 years of records (Table 4; Fig. 2).

## 4. Discussion

We used existing population data from native, augmented, and reintroduced Rocky Mountain bighorn sheep populations to determine the status of Rocky Mountain bighorn sheep populations across their range. Bighorn sheep populations have recovered in a number of areas in western North America due to extensive protections and translocation efforts (Boyce and Kausman, 2018). We found that the majority of Rocky Mountain bighorn sheep populations were increasing across their range based on both intrinsic rates of increase and proportional change in the last 5 years of records. That said, the average percent decline overshadowed average percent increase in the last 5 years of



**Fig. 1.** The distribution of varying intrinsic rates of increase estimates ( $r$ ) and density dependence estimates ( $d$ ) for Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) populations modelled across the United States and Canada. Light grey represent positive values and dark grey points represent negative values. Points were sized based on the magnitude of each parameter. Point size was locked when estimate values exceeded 0.05 for visual interpretation purposes.



**Fig. 2.** The distribution of percent change in population estimates over the last 5 years of records for all Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) populations, reintroduced populations, native populations, and augmented populations modelled across the United States and Canada. Light grey represent positive values and dark grey points represent negative values. Points were sized based on the magnitude of change. Point size was locked when percent change exceeded 100% for visual interpretation purposes.

**Table 2**

Moran's *I* results for density dependence, intrinsic rate of increase, and percent change in the last 5 years of records. We used approximate latitudes and longitudes of population ranges for Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) modelled across the United States and Canada to assess spatial autocorrelation among populations by comparing the observed Moran's *I* value to that expected from completely independent data.

Parameter	Observed	Expected	Standard deviation	p-Value
Density dependence	0.003	-0.005	0.011	0.459
Intrinsic rate of increase	0.023	-0.005	0.017	0.100
Percent change in the last 5 years of records	0.023	-0.005	0.017	0.057

records across multiple jurisdictions, highlighting the threat of localized extirpations for a number of populations across Rocky Mountain bighorn sheep range. Some of the largest declines in the last 5 years of records were found in reintroduced populations, which can be highly

susceptible to decline and extirpation, potentially attributable to ties to founder size, distance to domestic sheep (*O. aries*), and source stock for translocation (Shannon et al., 2014; Singer et al., 2000b). Massive die-offs tied to pneumonia outbreaks have been recorded across a number of US populations (Cassirer et al., 2018; Wild Sheep Working Group, 2012). Small populations like those following an introduction are more susceptible to disease-induced extirpation (Castro and Bolker, 2005). Cassirer et al. (2018) estimated a median of 48% declines in populations experiencing pneumonia outbreaks across a large portion of bighorn range. While this is nearly double the median decline in population size we observed in the last 5 years of records, it is still likely that a number of population declines were tied to pneumonia die-offs. More subtle declines in population size were likely tied to natural population fluctuations or slower drivers of population decline like increased predation pressure (Popp et al., 2014; Rominger et al., 2004), human-wildlife conflicts (Kindall et al., 2011; Popp et al., 2014), and changes in forage availability (Conner et al., 2018). Numerous covariates are involved in population fluctuations within a single population, and

**Table 3**

Linear model coefficients for predictors of change in population intrinsic rate of increase, density dependence, and percent change in the last 5 years of records for Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) modelled across the United States and Canada.

Variable	Estimate	SE	t-Value	P
<i>Intrinsic rate of increase</i>				
Translocation status (Reintroduced-Native)	-0.006	0.001	-4.713	< 0.001
Translocation status (Reintroduced-Augmented)	-0.005	0.001	-4.044	< 0.001
Translocation status (Native-Augmented)	$-5.844 \times 10^{-4}$	0.001	0.402	0.688
Latitude	$1.927 \times 10^{-5}$	$1.155 \times 10^{-4}$	0.167	0.867
Longitude	$-6.940 \times 10^{-6}$	$2.179 \times 10^{-5}$	-0.319	0.750
Data length	$1.086 \times 10^{-4}$	$3.614 \times 10^{-5}$	3.004	0.003
Number of records	$5.974 \times 10^{-5}$	$5.780 \times 10^{-4}$	1.034	0.303
<i>Density dependence</i>				
Translocation status (Reintroduced-Native)	-0.006	0.003	-1.912	0.057
Translocation status (Reintroduced-Augmented)	-0.003	0.003	-0.923	0.357
Translocation status (Native-Augmented)	-0.003	0.004	0.798	0.426
Latitude	$-3.695 \times 10^{-4}$	$3.098 \times 10^{-4}$	-1.193	0.234
Longitude	$1.938 \times 10^{-5}$	$5.845 \times 10^{-5}$	0.332	0.741
Data length	$5.917 \times 10^{-5}$	$9.676 \times 10^{-5}$	0.611	0.542
Number of records	$8.454 \times 10^{-5}$	$1.548 \times 10^{-4}$	0.546	0.586
<i>Percent change in last 5 years of records</i>				
Translocation status (Reintroduced-Native)	16.722	8.127	2.058	0.041
Translocation status (Reintroduced-Augmented)	-11.799	8.516	-1.386	0.168
Translocation status (Native-Augmented)	-28.521	9.614	-2.967	0.003
Data length	0.118	0.239	0.495	0.621
Number of records	-0.594	0.382	-1.554	0.122
PCNM1	-6.131	44.570	-0.138	0.891
PCNM2	22.979	43.970	0.523	0.602
PCNM3	82.278	48.452	1.698	0.091
PCNM4	47.918	44.671	1.073	0.285

**Table 4**

Percent change in populations over the last 5 years of records for all reintroduced, native, and augmented populations of Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) modelled across the United States and Canada.

State	Population trend			Average percent increase		Average percent decrease	
	Increasing	Decreasing	Extirpated	Avg.	SE	Avg.	SE
<b>Reintroduced</b>							
British Columbia	0	1	0	-	-	13	-
Colorado	29	9	2	16	3	18	6
Idaho	3	2	0	23	12	48	9
Montana	9	12	0	48	19	55	8
New Mexico	4	2	0	84	27	32	26
North Dakota	4	4	0	26	7	17	5
South Dakota	1	1	0	15	-	33	-
Oregon	4	2	2	45	14	49	3
Utah	6	0	2	16	5	-	-
Washington	6	3	1	46	15	18	3
Wyoming	2	3	0	27	26	16	6
All reintroduced	68	39	7	30	4	33	4
<b>Native</b>							
Alberta	3	4	0	25	10	5	3
British Columbia	3	4	0	15	12	22	4
Colorado	10	4	0	17	7	27	16
Idaho	3	0	0	38	16	-	-
Montana	11	7	0	86	22	30	8
Wyoming	2	2	0	7	5	16	9
All native	32	21	0	42	10	22	4
<b>Augmented</b>							
Alberta	3	0	0	15	3	-	-
British Columbia	0	4	0	-	-	40	10
Colorado	10	13	0	9	2	13	3
Idaho	0	3	0	-	-	14	6
Montana	2	4	0	27	< 1	34	17
All augmented	15	24	0	13	2	21	4
All populations	115	84	7	31	4	27	3

further assessments are required to identify drivers of decline within given regions. Our study provides a repository of population models that can be used to investigate drivers of change in populations of interest.

While the majority of native and reintroduced populations were

increasing, augmented populations tended to decline in the last 5 years of records. Augmentation is often used to reinforce populations of concern by increasing population number and growth (IUCN, 2013), and account for 27% of animal translocations in North America (Brichieri-Colombi and Moehrenschlager, 2016). While more detailed

**Table 5**

Average intrinsic rate of increase ( $r$ ) and density dependence ( $d$ ) across native, reintroduced, and supplemented populations Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) modelled across the United States and Canada.

	Average intrinsic rate of increase ( $r$ )		Average density dependence ( $d$ )	
	Avg.	SD	Avg.	SD
Native	0.006	0.004	-0.008	0.025
Reintroduced	0.013	0.020	0.0003	0.015
Supplemented	0.007	0.004	-0.003	0.010

investigation into augmentation timing and numbers would be beneficial, our investigation of population change in the last 5 years of records suggests that augmentation may not be effectively boosting population growth for many Rocky Mountain bighorn sheep populations. Previous assessments of augmentation efforts have shown low or mixed success for many species (Fischer and Lindenmayer, 2000; Griffith et al., 1989). While many papers have shown that augmented animals may have a better chance of survival when there are already established populations (e.g., Jesmer et al., 2018), translocated individuals can experience difficulties assimilating into already established populations (Danielson and Gaines, 1987; Poirier and Festa-Bianchet, 2018; Van Zant and Wooten, 2003). Robinson et al. (2019) found low mixing between augmented and resident Rocky Mountain bighorn sheep across multiple populations in Utah. A study of augmented bighorn sheep in Alberta, Canada found that translocated sheep required at least 1 year to integrate into the local population, experienced lower weight gains, and took at least 3 years to give birth (Poirier and Festa-Bianchet, 2018). Future studies should contrast various translocation protocols (e.g., Taylor et al., 2017), source herds (e.g., Whiting et al., 2012), population management, habitat quality, and disease outbreak status to further understand factors that might improve augmentation success. Similarly, comparisons could be made among populations with different numbers of augmentations. Alternatively, priority could be given to better understanding underlying drivers of decline within a population. Investment into re-establishing populations following intensive management of exogenous drivers of population decline will be a more effective use of resources than translocation for the purpose of reinforcing populations in distress when population declines are not driven by population dynamics (e.g., low genetic diversity).

Highly positive intrinsic rates of increase across reintroduced populations suggest population numbers tend to increase following re-introduction. This, combined with the fact that the majority of reintroduced populations were increasing in the last five years of records, suggests introductions may be relatively successful across bighorn sheep range. An earlier study conducted by Singer et al. (2000b) found relatively low introduction success across desert and Rocky Mountain bighorn sheep subspecies in the southwest based on a minimum viable population size classification of 'success.' Our results may reflect increasing knowledge, investments, and improvements in translocation protocols in recent decades (Brewer et al., 2014), though over half of our populations were reintroduced before 1980. Alternatively, population success may be tied to increasingly effective habitat management. There have been increasing efforts to prevent disease spread between domestic and wild sheep (Bureau of Land Management, 2016; Wild Sheep Working Group, 2012), and an emphasis on creating suitable habitat for reintroduced populations (Clapp and Beck, 2016; Singer et al., 2000b). That said, it is likely that reports and data sources we used tended toward reporting successful introductions and currently surviving populations of bighorn sheep, rather than reporting unsuccessful introductions and extirpations, which may bias our results toward more positive introduction outcomes.

There has been an increasing emphasis on broad-scale conservation and restoration across the globe (Rouget et al., 2006; Watson et al.,

2017). The ecosystems that we aim to conserve rarely fall within jurisdictional boundaries, but rather span management units, states, countries, and continents. Increasingly, species conservation and management strategies are beginning to represent multi-jurisdictional cooperative efforts (e.g., Gaden et al., 2008; Racey et al., 1999). Moreover, there is a push to establish global species monitoring programs and generate global species databases to facilitate broad-scale conservation efforts (e.g., Pereira and Cooper, 2006; Schmeller et al., 2015). Amalgamating multi-jurisdictional population data can assist in assessing the status of a wildlife species across their range, and understanding broad-scale management outcomes for species conservation. Local data are difficult to scale with regional and continental patterns and processes that shape ecosystems and communities (Allen et al., 2016; May, 1994). Broad-scale assessments like ours can reveal underlying trends and shifting patterns that are not detectable from a local perspective (e.g., Donovan et al., 2017; Roberts et al., 2019). This approach was particularly effective in the case of bighorn sheep, where interagency and jurisdictional collaborations have already established extensive cross-range species records (e.g., Wild Sheep Working Group, 2015). That said, establishing consistent methodologies across jurisdictions would increase our ability to assess population patterns across species range (e.g., population viability analysis tied to population sizes) and among previous studies of bighorn sheep population trends. More consistent monitoring and reporting of population numbers and stressors, like pneumonia die-offs, would assist in more thorough population modelling and assessment. For instance, while we were able to compare trends in the last 5 years of the most recently reported records for each population, not all records covered the same time windows nor reported the same stressors. This makes recent drivers of declines difficult to assess across species range because the last 5 years of records for some populations may be less recent than others and records on stressors differ among populations. Lack of data availability, variability in data collection techniques, and statistical issues in combining data sets of variable temporal coverage, are among some of the issues that confound current efforts for large-scale conservation and restoration (Balmford et al., 2003). Continued efforts toward multi-jurisdictional collaborations on monitoring and data sharing will be important for the advancement of broad-scale conservation.

A list of reports and articles used to collect population counts and estimates (Appendix A), a sample manager survey (Appendix B), a summary of data collected for each population (Appendix C), an in-depth description of modelling methods (Appendix D), a summary of population model outputs (Appendix E), a plot of each population's data and model (Appendix F), a discussion on outlier removal in the linear model for intrinsic rate of increase (Appendix G), and the results of a population trends hot-spot analysis (Appendix H) are available in the supplementary data. Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2020.108639>.

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**Victoria Donovan:** Conceptualisation, Methodology, Formal analysis, Investigation, Data curation, Writing - original draft, Writing - review & editing, Visualization, Project administration. **Caleb Roberts:** Conceptualisation, Methodology, Investigation, Writing - review & editing, Visualization. **Carissa Wonkka:** Conceptualisation, Methodology, Formal analysis, Writing - review & editing, Visualization. **Jeffrey Beck:** Methodology, Writing - review & editing. **Jesse Popp:** Methodology, Writing - review & editing. **Craig Allen:** Investigation, Writing - review & editing, Funding acquisition. **Dirac Twidwell:** Investigation, Writing - review & editing, Funding acquisition.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## References

Allen, C.R., Angeler, D.G., Cumming, G.S., Folke, C., Twidwell, D., Uden, D.R., 2016. Quantifying spatial resilience. *J. Appl. Ecol.* 53, 625–635. <https://doi.org/10.1111/1365-2664.12634>.

Baillie, S.R., Sutherland, W.J., Freeman, S.N., Gregory, R.D., Paradis, E., 2000. Consequences of large-scale processes for the conservation of bird populations. *J. Appl. Ecol.* 37, 88–102. <https://doi.org/10.1046/j.1365-2664.2000.00555.x>.

Balmford, A., Green, R.E., Jenkins, M., 2003. Measuring the changing state of nature. *Trends Ecol. Evol.* 18, 326–330. [https://doi.org/10.1016/S0169-5347\(03\)00067-3](https://doi.org/10.1016/S0169-5347(03)00067-3).

Bangs, E.E., Fritts, S.H., 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. *Wildl. Soc. Bull.* 24, 402–413.

Borcard, D., Legendre, P., 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices. *Ecol. Model.* 153, 51–68. [https://doi.org/10.1016/S0304-3800\(01\)00501-4](https://doi.org/10.1016/S0304-3800(01)00501-4).

Borcard, D., Legendre, P., Drapeau, P., 1992. Partitioning out the spatial component of ecological variation. *Ecology* 73, 1045–1055.

Borcard, D., Legendre, P., Avois-Jacquet, C., Tuomisto, H., 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology* 85, 1826–1832.

Boyce, M.S., Krausman, P.R., 2018. Controversies in mountain sheep management. *J. Wildl. Manag.* 82, 5–7. <https://doi.org/10.1002/jwmg.21400>.

Brewer, C.E., Bleich, V.C., Foster, J.A., Hosch-Hebden, T., McWhirter, D.E., Rominger, E.M., Wagner, M.W., Wiedmann, B.P., 2014. Bighorn Sheep: Conservation Challenges and Management Strategies for the 21st Century. Wild Sheep Working Group, Western Association of Fish and Wildlife Agencies, Cheyenne, Wyoming, USA.

Brichieri-Colombi, T.A., Moehrenschlager, A., 2016. Alignment of threat, effort, and perceived success in North American conservation translocations. *Conserv. Biol.* 30, 1159–1172.

Buechner, H.K., 1960. The bighorn sheep in the United States, its past, present, and future. *Wildl. Monogr.* 4, 3–174.

Bureau of Land Management, 2016. Management of Domestic Sheep and Goats to Sustain Wild Sheep (No. MS 1730). United States Department of Interior, Bureau of Land Management.

Cassirer, E.F., Manlove, K.R., Almberg, E.S., Kamath, P.L., Cox, M., Wolff, P., Roug, A., Shannon, J., Robinson, R., Harris, R.B., 2018. Pneumonia in bighorn sheep: risk and resilience. *J. Wildl. Manag.* 82, 32–45.

Castro, F.D., Bolker, B., 2005. Mechanisms of disease-induced extinction. *Ecol. Lett.* 8, 117–126. <https://doi.org/10.1111/j.1461-0248.2004.00693.x>.

Ceballos, G., Ehrlich, P.R., 2002. Mammal population losses and the extinction crisis. *Science* 296, 904–907. <https://doi.org/10.1126/science.1069349>.

Clapp, J.G., Beck, J.L., 2016. Short-term impacts of fire-mediated habitat alterations on an isolated bighorn sheep population. *Fire Ecol.* 12, 80–98. <https://doi.org/10.4996/fireecology.1203080>.

Clapp, J.G., Beck, J.L., Gerow, K.G., 2014. Post-release acclimation of translocated low-elevation, non-migratory bighorn sheep. *Wildl. Soc. Bull.* 38, 657–663. <https://doi.org/10.1002/wsb.441>.

Colchero, F., Medellin, R.A., Clark, J.S., Lee, R., Katul, G.G., 2009. Predicting population survival under future climate change: density dependence, drought and extraction in an insular bighorn sheep. *J. Anim. Ecol.* 78, 666–673. <https://doi.org/10.1111/j.1365-2656.2009.01528.x>.

Collen, B., Loh, J., Whitmee, S., McRae, L., Amin, R., Baillie, J.E.M., 2009. Monitoring change in vertebrate abundance: the living planet index. *Conserv. Biol.* 23, 317–327. <https://doi.org/10.1111/j.1523-1739.2008.01117.x>.

Collen, B., McRae, L., Deinet, S., De Palma, A., Carranza, T., Cooper, N., Loh, J., Baillie, J.E.M., 2011. Predicting how populations decline to extinction. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 366, 2577–2586. <https://doi.org/10.1098/rstb.2011.0015>.

Conner, M.M., Stephenson, T.R., German, D.W., Monteith, K.L., Few, A.P., Bair, E.H., 2018. Survival analysis: informing recovery of Sierra Nevada bighorn sheep. *J. Wildl. Manag.* 82, 1442–1458. <https://doi.org/10.1002/jwmg.21490>.

Cook, C., Possingham, H.P., Fuller, R.A., 2014. Contribution of systematic reviews to management decisions. *Conserv. Biol.* 27, 902–915. <https://doi.org/10.1111/cobi.12114>.

Danielson, B.J., Gaines, M.S., 1987. The influences of conspecific and heterospecific residents on colonization. *Ecology* 68, 1778–1784. <https://doi.org/10.2307/1939869>.

Donovan, V.M., Wonkka, C.L., Twidwell, D., 2017. Surging wildfire activity in a grassland biome. *Geophys. Res. Lett.* 44, 2017GL072901. <https://doi.org/10.1002/2017GL072901>.

Dray, S., Legendre, P., Peres-Neto, P.R., 2006. Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM). *Ecol. Model.* 196, 483–493. <https://doi.org/10.1016/j.ecolmodel.2006.02.015>.

Ewen, J.G., Armstrong, D.P., Parker, K.A., Seddon, P.J., 2011. *Reintroduction Biology: Integrating Science and Management*. John Wiley & Sons, Chichester, UK.

Festa-Bianchet, M., Coulson, T., Gaillard, J.-M., Hogg, J.T., Pelletier, F., 2006. Stochastic predation events and population persistence in bighorn sheep. *Proc. R. Soc. B Biol. Sci.* 273, 1537–1543. <https://doi.org/10.1098/rspb.2006.3467>.

Fischer, J., Lindenmayer, D.B., 2000. An assessment of the published results of animal relocations. *Biol. Conserv.* 96, 1–11. [https://doi.org/10.1016/S0006-3207\(00\)00048-3](https://doi.org/10.1016/S0006-3207(00)00048-3).

Gaden, M., Krueger, C., Goddard, C., Barnhart, G., 2008. A joint strategic plan for management of Great Lakes fisheries: a cooperative regime in a multi-jurisdictional setting. *Aquat. Ecosyst. Health Manag.* 11, 50–60. <https://doi.org/10.1080/14634980701877043>.

George, J.L., Kahn, R., Miller, M.W., Watkins, B., 2009. Colorado bighorn sheep management plan 2009–2019 (No. 81). Colorado Division of Wildlife, Department of Natural Resources, Denver, Colorado.

Getis, A., Ord, J.K., 1992. The analysis of spatial association by use of distance statistics. *Geogr. Anal.* 24, 189–206. <https://doi.org/10.1111/j.1538-4632.1992.tb00261.x>.

Gompertz, B., 1825. On the nature of the function expressive of the law of human mortality, and on a new mode of determining the value of life contingencies. *Philos. Trans. R. Soc. Lond.* 115, 513–583.

Griffith, B., Scott, J.M., Carpenter, J.W., Reed, C., 1989. Translocation as a species conservation tool: status and strategy. *Science* 245, 477–480. <https://doi.org/10.1126/science.245.4917.477>.

IUCN (World Conservation Union), 1987. *Position Statement on the Translocation of Living Organisms: Introductions, Reintroductions, and Re-stocking*. IUCN, Gland, Switzerland.

IUCN/SSC, 2013. *Guidelines for Reintroductions and Other Conservation Translocations*. IUCN Species Survival Commission, Gland, Switzerland.

Jesmer, B.R., Merkle, J.A., Goheen, J.R., Aikens, E.O., Beck, J.L., Courtemanch, A.B., Hurley, M.A., McWhirter, D.E., Miyasaki, H.M., Monteith, K.L., Kauffman, M.J., 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. *Science* 361, 1023–1025. <https://doi.org/10.1126/science.aaat0985>.

Kindall, J.L., Muller, L.I., Clark, J.D., Lupardus, J.L., Murrow, J.L., 2011. Population viability analysis to identify management priorities for reintroduced elk in the Cumberland Mountains, Tennessee. *J. Wildl. Manage.* 75, 17451752. <https://doi.org/10.1002/jwmg.226>.

Koops, D.N., Colchero, F., Hersey, K., Gimenez, O., 2015. Disentangling the effects of climate, density dependence, and harvest on an iconic large herbivore's population dynamics. *Ecol. Appl.* 25, 956–967.

Krausman, P.R., 2000. An introduction to the restoration of bighorn sheep. *Restor. Ecol.* 8, 3–5. <https://doi.org/10.1046/j.1526-100x.2000.80060.x>.

Lajeunesse, M.J., Forbes, M.R., 2003. Variable reporting and quantitative reviews: a comparison of three meta-analytical techniques. *Ecol. Lett.* 6, 448–454. <https://doi.org/10.1046/j.1461-0248.2003.00448.x>.

Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673. <https://doi.org/10.2307/1939924>.

Levins, R., 1966. The strategy of model building in population biology. *Am. Sci.* 54, 421–431.

Loh, J., Green Rhys, E., Taylor, Ricketts, John, Lamoreux, Martin, Jenkins, Valerie, Kapos, Jorgen, Randers, 2005. The Living Planet Index: using species population time series to track trends in biodiversity. *Philos. Trans. R. Soc. Lond. Ser. B Biol. Sci.* 360, 289–295. <https://doi.org/10.1098/rstb.2004.1584>.

May, R.M., 1994. The effects of spatial scale on ecological questions and answers. In: Edwards, P.J., May, R.M., Webb, N.R. (Eds.), *Large-scale Ecology and Conservation Biology*. Blackwell Scientific, London, UK, pp. 1–18.

Montana Fish, Wildlife, and Parks (MFWP), 2009. *Montana Bighorn Sheep Conservation Strategy*. Montana Fish, Wildlife, and Parks, Wildlife Bureau, Helena, Montana.

Noon, B.R., McKelvey, K.S., Dickson, B.G., 2009. Multispecies conservation planning on U.S. federal lands. In: Millspaugh, J.J., Thompson III, R. (Eds.), *Models for Planning Wildlife Conservation in Large Landscapes*. Academic Press, New York, NY, US, pp. 51–84.

Noon, B.R., Bailey, L.L., Sisk, T.D., McKelvey, K.S., 2012. Efficient species-level monitoring at the landscape scale. *Conserv. Biol.* 26, 432–441. <https://doi.org/10.1111/j.1523-1739.2012.01855.x>.

Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., Minchin, P.R., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Szoecs, E., Wagner, H., 2019. *vegan: Community Ecology Package*. R Package Version 2.5-4.

Ord, J.K., Getis, A., 1995. Local spatial autocorrelation statistics: distributional issues and an application. *Geogr. Anal.* 27, 286–306. <https://doi.org/10.1111/j.1538-4632.1995.tb00912.x>.

Paradis, E., Schliep, K., 2018. *ape 5.0: an environment for modern phylogenetics and*

evolutionary analyses in R. *Bioinformatics* 35, 526–528.

Pereira, H.M., Cooper, D.H., 2006. Towards the global monitoring of biodiversity change. *Trends Ecol. Evol.* 21, 123–129. <https://doi.org/10.1016/j.tree.2005.10.015>.

Plummer, M., 2003. JAGS: a program for analysis of Bayesian graphical models using Gibbs sampling. In: Proceedings of the 3rd International Workshop on Distributed Statistical Computing. 124. pp. 1–10.

Poirier, M.-A., Festa-Bianchet, M., 2018. Social integration and acclimation of translocated bighorn sheep (*Ovis canadensis*). *Biol. Conserv.* 218, 1–9. <https://doi.org/10.1016/j.biocon.2017.11.031>.

Popp, J.N., Toman, T., Mallory, F.F., Hamr, J., 2014. A century of elk restoration in eastern North America. *Restor. Ecol.* 22, 723–730. <https://doi.org/10.1111/rec.12150>.

R Core Team, 2017. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Racey, G., Harris, A., Gerrish, L., Armstrong, E., McNicol, J., Baker, J., 1999. Forest Management Guidelines for the Conservation of Woodland Caribou: A Landscape Approach. Ontario Ministry of Natural Resources, Thunder Bay, Ontario (MS draft).

Roberts, C.P., Allen, C.R., Angeler, D.G., Twidwell, D., 2019. Shifting avian spatial regimes in a changing climate. *Nat. Clim. Chang.* 9, 562–566. <https://doi.org/10.1038/s41558-019-0517-6>.

Robinson, R.W., Whiting, J.C., Shannon, J.M., Olson, D.D., Flinders, J.T., Smith, T.S., Bowyer, R.T., 2019. Habitat use and social mixing between groups of resident and augmented bighorn sheep. *Sci. Rep.* 9, 1–12. <https://doi.org/10.1038/s41598-019-51370-y>.

Rominger, E.M., Whitlaw, H.A., Weybright, D.L., Dunn, W.C., Ballard, W.B., 2004. The influence of mountain lion predation on bighorn sheep translocations. *J. Wildl. Manag.* 68, 993–999.

Rouget, M., Cowling, R.M., Lombard, A.T., Knight, A.T., Kerley, G.I.H., 2006. Designing large-scale conservation corridors for pattern and process. *Conserv. Biol.* 20, 549–561. <https://doi.org/10.1111/j.1523-1739.2006.00297.x>.

Schlossberg, S., King, D.I., 2009. Modeling animal habitats based on cover types: a critical review. *Environ. Manag.* 43, 609–618. <https://doi.org/10.1007/s00267-008-9159-6>.

Schmeller, D.S., Julliard, R., Bellingham, P.J., Böhm, M., Brummitt, N., Chiarucci, A., Couvet, D., Elmendorf, S., Forsyth, D.M., Moreno, J.G., Gregory, R.D., Magnusson, W.E., Martin, L.J., McGeoch, M.A., Mihoub, J.-B., Pereira, H.M., Proença, V., van Swaay, C.A.M., Yahara, T., Belnap, J., 2015. Towards a global terrestrial species monitoring program. *J. Nat. Conserv.* 25, 51–57. <https://doi.org/10.1016/j.jnc.2015.03.003>.

Schmidt, J.L., Gilbert, D.L., 1978. Big Game of North America: Ecology and Management. Stackpole Books, Harrisburg, PA.

Seddon, P.J., 2010. From reintroduction to assisted colonization: moving along the conservation translocation spectrum. *Restor. Ecol.* 18, 796–802.

Shannon, J.M., Whiting, J.C., Larsen, R.T., Olson, D.D., Flinders, J.T., Smith, T.S., Bowyer, R.T., 2014. Population response of reintroduced bighorn sheep after observed commingling with domestic sheep. *Eur. J. Wildl. Res.* 60, 737–748. <https://doi.org/10.1007/s10344-014-0843-y>.

Singer, Francis J., Bleich, V.C., Gudorf, M.A., 2000a. Restoration of bighorn sheep metapopulations in and near western national parks. *Restor. Ecol.* 8, 14–24.

Singer, Francis J., Papouchis, C.M., Symonds, K.K., 2000b. Translocations as a tool for restoring populations of bighorn sheep. *Restor. Ecol.* 8, 6–13. <https://doi.org/10.1046/j.1526-100x.2000.80061.x>.

Stephen, C.L., Whittaker, D.G., Gillis, D., Cox, L.L., Rhodes, O.E., 2005. Genetic consequences of reintroductions: an example from Oregon pronghorn antelope (*antilocapra americana*). *J. Wildl. Manag.* 69, 1463–1474.

Su, Y.-S., Yajima, M., 2015. R2jags: Using R to Run “JAGS”. R Package Version 0.5-7.

Swan, K.D., Lloyd, N.A., Moehrenschlager, A., 2018. Projecting further increases in conservation translocations: a Canadian case study. *Biol. Conserv.* 228, 175–182.

Taylor, G., Canessa, S., Clarke, R.H., Ingwersen, D., Armstrong, D.P., Seddon, P.J., Ewen, J.G., 2017. Is reintroduction biology an effective applied science? *Trends Ecol. Evol.* 32, 873–880. <https://doi.org/10.1016/j.tree.2017.08.002>.

Van Zant, J.L., Wooten, M.C., 2003. Translocation of Choctawhatchee beach mice (*Peromyscus polionotus allophrys*): hard lessons learned. *Biol. Conserv.* 112, 405–413. [https://doi.org/10.1016/S0006-3207\(02\)00338-5](https://doi.org/10.1016/S0006-3207(02)00338-5).

Wang, G., Hobbs, N.T., Twombly, S., Boone, R.B., Illius, A.W., Gordon, I.J., Gross, J.E., 2008. Density dependence in northern ungulates: interactions with predation and resources. *Popul. Ecol.* 51, 123. <https://doi.org/10.1007/s10144-008-0095-3>.

Watson, D.M., Doerr, V.A.J., Banks, S.C., Driscoll, D.A., van der Ree, R., Doerr, E.D., Sunnucks, P., 2017. Monitoring ecological consequences of efforts to restore landscape-scale connectivity. *Biol. Conserv.* 206, 201–209. <https://doi.org/10.1016/j.biocon.2016.12.032>.

Weilenmann, M., Gusset, M., Mills, D.R., Gabanapelo, T., Schiess-Meier, M., 2011. Is translocation of stock-raiding leopards into a protected area with resident conspecifics an effective management tool? *Wildl. Res.* 37, 702–707. <https://doi.org/10.1071/WR10013>.

Weise, F.J., Stratford, K.J., van Vuuren, R.J., 2014. Financial costs of large carnivore translocations – accounting for conservation. *PLoS One* 9. <https://doi.org/10.1371/journal.pone.0105042>.

White, P.J., Lemke, T.O., Tyers, D.B., Fuller, J.A., 2008. Initial effects of reintroduced wolves *Canis lupus* on bighorn sheep *Ovis canadensis* dynamics in Yellowstone National Park. *Wildl. Biol.* 14, 138–146. [https://doi.org/10.2981/0909-6396\(2008\)14\[138:IEORWC\]2.0.CO;2](https://doi.org/10.2981/0909-6396(2008)14[138:IEORWC]2.0.CO;2).

Whiting, J.C., Olson, D.D., Shannon, J.M., Bowyer, R.T., Klaver, R.W., Flinders, J.T., 2012. Timing and synchrony of births in bighorn sheep: implications for re-introduction and conservation. *Wildl. Res.* 39, 565572. <https://doi.org/10.1071/WR12059>.

Wild Sheep Working Group, 2012. Recommendations for Domestic Sheep and Goat Management in Wild Sheep Habitat. Western Association of Fish Wildlife Agencies.

Wild Sheep Working Group, 2015. Records of Wild Sheep Translocations- United States and Canada, 1922–Present. Western Association of Fish Wildlife Agencies, USA.