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Translocated to the fringe: genetic and niche variation in bighorn sheep of the Great Basin and northern Mojave deserts

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ABSTRACT

Aim Conservation biologists use various approaches to augment imperilled populations in order to supplement genetic variation and restore ecological function. However, understanding genotypic, phenotypic and ecotypic variation is critical in determining the most suitable sources to conserve historical and functional variation. Bighorn sheep (*Ovis canadensis*) provide a classic example of restoration biology, where management programmes have re-established extirpated populations via translocations. Through this process, translocated individuals may now face novel environments, including new bioclimatic conditions and an opportunity to interbreed with historically isolated and distinct genetic units. Our goal was to integrate genetic and ecological analyses to assess some of the evolutionary ramifications of this important management practice.

Location Western North America, but focused on the Great Basin and northern Mojave deserts.

Methods We quantified genetic variation across 55 Herds of bighorn sheep using 16 microsatellite loci ($N = 347$) and a mitochondrial gene ($N = 110$). We used ordination, Bayesian clustering and phylogenetic analyses to delineate evolutionary units. We used multivariate ordination for 26 ecologically relevant variables to characterize niche-based differences among genetic clusters and then tested whether repatriated populations occupy conditions similar to source areas.

Results We document genetic differentiation among three traditional management units of bighorn sheep that now occupy the Great Basin and northern Mojave deserts, but also identify limited hybridization among these groups. Niche-based analyses revealed that translocated populations now occur in conditions incongruent with source ranges.

Main conclusions This study highlights the importance of considering both genetic variation and ecological differences when implementing translocations. Early consideration of these variables may help minimize the potential for hybridization among distinct groups and mitigate challenges of managing populations experiencing novel environments. More broadly, results from this study have implications for future restoration efforts in this iconic system, but also for similar translocation-based conservation programmes.

Keywords

Admixture, assisted migration, conservation genetics, managed relocation, non-analogue niche, translocation.

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INTRODUCTION

Many populations are experiencing declines (Thomas *et al.*, 2004), and although some may recover, others, and perhaps entire communities, may require intervention to restore lost diversity, adaptive variation and ecological function (Hoegh-Guldberg *et al.*, 2008; Richardson *et al.*, 2009; Thomas *et al.*, 2013). Options include population augmentation by introducing genetic stock from other regions to increase genetic diversity and managed relocation (or assisted colonization/migration) to re-establish extirpated populations. These efforts can improve population viability, restore biodiversity (Brooks, 2010) and recover lost ecosystem function (Donlan *et al.*, 2005, 2006). Successful establishment of newly translocated individuals requires that recipient areas have a suite of environmental and habitat characteristics (Osborne & Seddon, 2012) to which individuals are adapted or can quickly acclimate. Likewise, in situations where translocated individuals are expected to interbreed with residents, they would ideally be from appropriate genetic stock that augments diversity but avoids crossing between naturally isolated and distinct evolutionary lineages. Although planned genetic augmentation can sometimes benefit imperilled populations (Johnson *et al.*, 2010; Gompert, 2012; Miller *et al.*, 2012; Hedrick, 2013), programmes typically avoid admixture between differentiated groups (Allendorf *et al.*, 2013). Fortunately, the ability to quantify both genetic variation and ecological differences within the context of evolutionary history is rapidly increasing (Richardson & Whittaker, 2010) and can yield valuable perspectives for conservation (Malaney & Cook, 2013; Moritz & Potter, 2013).

A particularly powerful approach is to use joint analyses to understand how well genotypic and ecotypic diversity has been managed as they relate to conservation biogeography (Ackerly *et al.*, 2010; Franklin, 2010; Richardson & Whittaker, 2010). This approach can provide essential insights and inform conservation activities, and new perspectives will be critical when contemplating contentious programmes including managed relocation (Hewitt *et al.*, 2011; Aitken & Whitlock, 2013) and facilitated adaptation (Thomas *et al.*, 2013). Although these programmes are controversial, they may become important management tools in the face of rapid change (Gillson *et al.*, 2013). We utilize the long history of wildlife translocations to gain key empirical insights into debates over rapidly evolving conservation-oriented action.

Bighorn sheep (*Ovis canadensis*) are among the most rare and iconic species of western North America and often prized as a game animal (Monteith *et al.*, 2013). This species has been part of the North American biota since the Pleistocene (Rezaei *et al.*, 2010), but by the mid-20th century, these large mammals suffered serious declines, and many populations were extirpated (Buechner, 1960). Extirpations were often the consequence of overharvest, livestock encroachment, disease, xerification, and other habitat changes (Seton, 1929; Wehausen, 1986; Valdez & Krausman, 1999). In a bold effort to re-establish populations, management agencies

enacted repatriation programmes (Singer *et al.*, 2000). Most translocations were predicated on morphologically based taxonomy (Cowan, 1940) with coarse reconstructions of historical distributions and ecological associations (Hall, 1946, 1981; Buechner, 1960; Shackleton, 1985). Repatriations relied on the availability of both funding and source populations (Krausman, 2000), with animals often originating from distant areas and potentially disparate ecological conditions. For example, managers moved individuals to the Great Basin from source areas in the Rocky Mountains and Canadian Rockies. Despite efforts to place bighorn sheep in similar physiographic and vegetation-based habitats (Johnson & Swift, 2000; Zeigenfuss *et al.*, 2000), long-distance translocations may have placed some populations in dissimilar climatic conditions, resulting in mismatches between physiological or life-history adaptations and local environmental conditions (Whiting *et al.*, 2011, 2012; Wiedmann & Sargeant, 2014). Furthermore, translocations from multiple source areas often brought previously isolated populations into close proximity, potentially facilitating interbreeding between distinct groups. In particular, early on, many translocated populations experienced poor recruitment (Krausman, 2000), potentially the result of demographic and genetic effects (Ramey *et al.*, 2000; Hedrick *et al.*, 2001; Whittaker *et al.*, 2004), and poor consideration of ecotypic variation (Whiting *et al.*, 2012; Wiedmann & Sargeant, 2014). Nevertheless, repatriation programmes have led to successful re-establishment of extirpated populations, especially across the Great Basin (NDOW, 2001). Considering the high number of transplants in this region, we sought to identify the genetic and niche-based characteristics of repatriated bighorn sheep. The well-documented history of repatriation provides an unparalleled opportunity to evaluate outcomes of previous decisions and gain key insights to guide future translocation programmes of wild sheep and other imperilled species.

The goal of this study was to explore the species–environment relationship within a highly managed taxon by quantifying genetic variation and characterizing niche-based variables in the translocated ranges. We focus on the Great Basin and northern Mojave deserts that harbour translocated, but now free-ranging bighorn sheep (Fig. 1). Specifically, we test for evidence of distinct genetic units and identify signals of post-translocation interbreeding. We then assess whether genetic units have discrete niche-based characteristics and compare occupied conditions to those found in source regions.

METHODS

Genetic samples

We obtained fresh tissues and faecal material from 55 Herds of bighorn sheep from throughout the Great Basin and Mojave deserts, which provided representation of the three management units that occupy the Nevada bighorn sheep

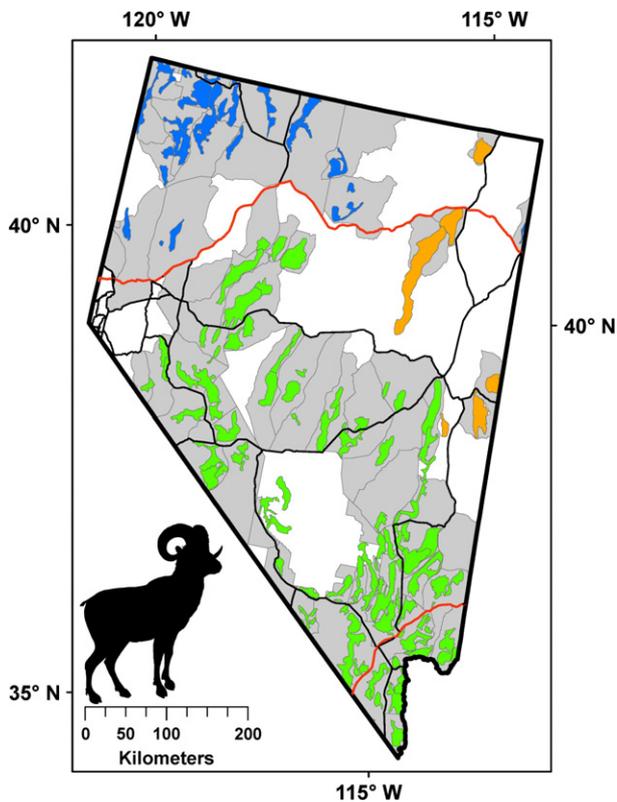


Figure 1 Distribution of bighorn sheep (*Ovis canadensis*) Herds in the study area with the occupied distribution of three management units shown in colour, and broader Nevada bighorn sheep management areas (NBSMAs) shown in grey, plus major highways (red and black lines). Blue – California bighorn sheep (CBS), green – desert bighorn sheep (DBS), orange – Rocky Mountain bighorn sheep (RMBS).

management areas (NBSMA). We use the term ‘management units’ to refer to traditionally recognized subspecies routinely used by natural-resource agencies for translocation activities. Translocations of bighorn sheep in Nevada began in 1968 and were based on Cowan (1940) taxonomy and modified by Hall (1946) to recognize seven subspecies. Within Nevada, three subspecies were originally geographically defined including *Ovis canadensis nelsoni* (desert bighorn sheep; DBS) in the south, *O. c. californiana* (California bighorn sheep; CBS) in the north-west and *O. c. canadensis* (Rocky Mountain bighorn sheep; RMBS) in the north-east. Consequently, DBS were repatriated throughout central Nevada from the northern Mojave desert, while RMBS were transplanted to north-eastern Nevada, originating from the Rocky Mountains, principally Colorado. At the time, CBS were thought to occur from the southern Sierra Nevada north to British Columbia (Cowan, 1940) and, consequently, British Columbia animals were translocated to north-western Nevada (NDOW, 2001; Olson *et al.*, 2013). More recent morphometric (Wehausen & Ramey, 1993) and genetic (Ramey, 1995) analyses suggest that Nevada originally contained only DBS.

Genetic data

Complete genetic protocols are available in the supplemental materials (see Appendix S1 in Supporting Information), but briefly, we generated genotypes for 347 individuals at 16 microsatellite loci. In all reactions, we included positive and negative controls with a minimum of two replicate analyses. We augmented our nuclear perspective of genetic diversity by generating mitochondrial DNA sequences from a subset of samples using primers designed for this project.

Genetic analyses

Genotypic clusters

To detect regional patterns of geographic subdivision within and among management units, we used principal coordinates analysis (PCoA) of genetic variation in GENALEX (Peakall & Smouse, 2006, 2012). We generated a pairwise genetic distance matrix of putatively identified samples that contained $k = 16$ eigenvalues (16 loci).

For an alternative characterization of genotypic clusters, we used Bayesian clustering (BC) to explore subdivisions without *a priori* grouping of samples. We used STRUCTURE v2.3.3 (Pritchard *et al.*, 2000) allowing for admixture (François & Durand, 2010) and correlated allele frequencies (Falusch *et al.*, 2003). We allowed K to vary 1 to 10 with ten replicates each, a burn-in period of 100,000 generations, and sampling for 1 million iterations. We identified the optimal K using the ΔK method (Evanno *et al.*, 2005) as implemented in STRUCTURE HARVESTER (Earl, 2012). Because the ΔK approach may underestimate the optimal number of clusters in the presence of hierarchical variation (Waples & Gaggiotti, 2006), we also heuristically examined the differences in log-likelihood values among simulations (Pritchard *et al.*, 2007). After identifying optimal clusters (Gilbert *et al.*, 2012), we summarized K with CLUMPP using the Greedy algorithm (Jakobsson & Rosenberg, 2007) and assessed cluster assignments applying a 0.90 probability (q) threshold. Samples that had partial assignment to two groups ($q < 0.90$ for any one group), with credibility intervals not encompassing zero for either group, were considered hybrids. Individuals with partial assignment to two groups but with credibility intervals encompassing zero were considered as potentially admixed. We set aside hybrid and potentially admixed individuals to quantify linkage disequilibrium and estimate differentiation among genetic units using F_{ST} and Nei’s corrected distance (D) (Nei, 1973; Hillis, 1984).

Phylogenetic reconstruction

We conducted phylogenetic analyses of the mtDNA dataset to understand the deeper biogeographic history of *O. canadensis* lineages. We determined the best-fit model of nucleotide substitution using the Bayesian information criterion (BIC) (Posada & Buckley, 2004) in jMODELTEST 2.1.4

(Posada, 2008; Darriba *et al.*, 2012) by exploring 88 models with default settings. We then reconstructed phylogenetic relationships under the best-fit model (HKY + I) using 1 million generations, sampling every 1000, starting with a random tree and run with four chains set to default heating conditions in MRBAYES v. 3.1.2 (Huelsenbeck & Ronquist, 2005; Lakner *et al.*, 2008). To polarize the character matrix, we used the sister taxon *Ovis dalli* and assessed convergence diagnostics by examining the optimal parameter estimates (ESS > 200) in TRACER v.1.5 (Drummond & Rambaut, 2007). Nodal support values were identified from the majority rules consensus of residual trees with 10% discarded as burn-in (Huelsenbeck & Imennov, 2002). To ensure replicated convergence, we completed three independent analyses and depicted the final consensus phylogram with FIGTREE v1.4.0 (Drummond & Rambaut, 2007).

Niche-based analyses

Sampling

Considering the extensive methodology associated with obtaining and processing niche-based variation and geographic samples, we present complete protocols in the supplemental materials (see Appendix S1). Our goals were to (1) characterize ecotypic differences among management units, (2) place differences within the context of spatial autocorrelation and (3) compare bioclimatic conditions of translocated areas to source ranges (British Columbia and Colorado). Consequently, we characterized the distribution of bighorn sheep using the actual and potential distributions from within the NBSMAs, all areas in the Great Basin and northern Mojave deserts (background), and from source regions.

Bioclimatic and physiographic features are important for the persistence of bighorn sheep (Epps *et al.*, 2004, 2007) and likely important in Grinnellian niche space (Soberón, 2007) and consequently the scenopoetic niche (Peterson *et al.*, 2011). Further, vegetation-based variables are important predictors for bighorn sheep prevalence. Therefore, we extracted niche-based variables for the three sets of randomly generated points. Variables included 19 bioclimatic variables (Hijmans *et al.*, 2005), elevation, slope, two land cover classifications, percentage tree-cover and indices of greenness (NDVI, NDVI-SD).

Ordination

Prior to analyses, we tested for highly correlated variables using a Pearson's *r* correlation coefficient across the matrix of 26 variables from 5000 random points and then reduced the dataset by removing 13 spatially auto-correlated variables [> 0.7] (McGarigal *et al.*, 2000). We used principal components analysis (PCA) to explore patterns of multidimensional environmental space (E-space) of scenopoetic variables (Peterson *et al.*, 2011). We conducted three separate PCAs:

(1) contrasting NBSMAs that coincide with the three genetic clusters identified in this study, (2) comparing areas actually or potentially occupied by bighorn sheep (NBSMA) to random background samples and (3) comparing translocated Herds to source areas. PCA matrices contained 13 eigenvalues, and we assessed the number of significant explanatory components (axes) using the significant deviation in eigenvalues criterion (Jackson, 1993). We conducted PCAs using the *prcomp* routine for R (Oksanen *et al.*, 2008; R Development Core Team, 2008) by centring scores, scaling variables for unit variance and varimax rotation. We then depicted the component scores and biplots of variable loadings for each PCA.

RESULTS

Sampling

Genetic diversity

The microsatellite dataset consisted of 347 samples that consistently amplified for all loci, and MICRO-CHECKER detected no inconsistencies in the dataset. All loci were polymorphic and most deviated from Hardy–Weinberg expectations when examined across the entire dataset and within major genetic subunits. However, these deviations may be the result of hierarchical subdivision within major genetic clusters (*i.e.* Wahlund effect) because loci failed to deviate from HWE within select well-sampled Herds (Table S1). Therefore, we retained all loci for analyses.

The mtDNA dataset contained 11 unique ND5 haplotypes with 19 variable sites and 17 that were parsimony informative. Haplotypes were minimally diverged with low nucleotide diversity ($\pi = 0.00341$) and mean nucleotide differences ($k = 4.030$).

Genetic analyses

Genetic clusters and clades

Multivariate ordination of nDNA showed three genetic clusters, largely consistent with current management units (Fig. 2). The PCoA revealed three vectors sufficient to explain 73.98% of observed genetic variation. Although the three management units were largely distinct, the PCoA revealed a small pool of potentially admixed individuals (Fig. 2). Further, three samples had nuclear genotypes unexpected from harvest location. Two putative RMBS, one from the Great Basin National Park Herd (Unit 115) and the other from the Badlands herd (Unit 74), had pure DBS genotypes. Finally, a putative DBS harvested from the White Pine herd (Unit 131) had a pure RMBS nuclear genotype.

Our phylogenetic analysis of mtDNA variation recovered three clades, although the relationship among these clades is not well supported (Fig. 3). The first clade (Desert) is exclusively found in individuals with a pure nuclear DBS genotype

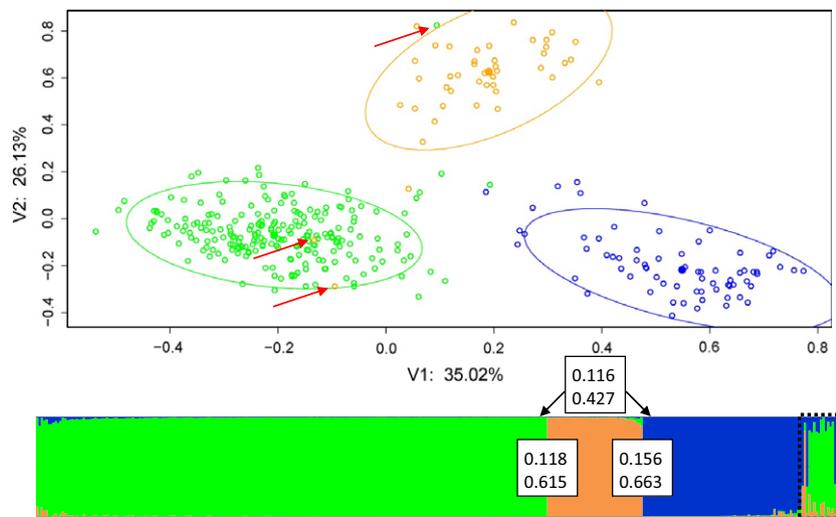


Figure 2 Genetic variation at 16 microsatellite loci in three management units of bighorn sheep (*Ovis canadensis*) within the Great Basin and northern Mojave deserts. Above: Scatter plot of principal coordinates analysis of genetic variation with 75% confidence ellipses: Blue = California bighorn sheep, green = Desert bighorn sheep, orange = Rocky Mountain bighorn sheep. The first two vectors (V) account for > 61% of genetic variation. Red arrows show three samples with field identifications (2 RMBS and 1 DBS) that are discordant with genotypes. Central to the three clusters is a pool of potentially admixed individuals. Below: *STRUCTURE* plot of Bayesian clusters ($K = 3$). Dashed black box shows 19 hybrid or potentially admixed individuals ($q < 0.90$). Assignments closely correspond to identifications of management units. Inset boxes show pairwise differentiation among genetic clusters with F_{ST} above and Nei's corrected distance below.

($N = 72$) or their hybrids (see below for designations). The other well-supported and well-represented clade (Cal-Rock) contains both pure nuclear CBS and RMBS individuals ($N = 17$ and $N = 4$, respectively) with a single potentially admixed individual. The third clade is poorly represented and recovered from four individuals from two Herds. We refer to this as a 'Rocky' clade because initial analyses suggest this clade is broadly distributed within the native range of RMBS (J. Wehausen unpubl. data), and our analyses recover this lineage at the margins of sampling in areas reflecting nDNA admixture (two pure nuclear DBS and two hybrids). Thus, we find clear mtDNA differentiation between DBS and at least one polyphyletic CBS-RMBS clade, supporting the close evolutionary affinity of the latter. The degree to which the polyphyletic CBS-RMBS pattern in the Cal-Rock clade represents unsorted ancestral polymorphism versus ongoing gene flow requires further exploration.

The ΔK analysis for the nDNA (Evanno *et al.*, 2005) showed a clear signal of hierarchical structure with the highest score at $K = 2$, and the second highest value at $K = 3$. At $K = 2$, we detect one cluster containing DBS and the other a combined CBS-RMBS cluster. At $K = 3$, the latter subdivided into distinct CBS and RMBS groups (Fig. 3; Figure S1). Genetic subdivision among the three clusters was moderate with $F_{ST} > 0.115$ and $D > 0.425$ (Fig. 3). Considering the degree of differentiation among the nDNA clusters, the results of phylogenetic analyses and the history of recognizing Cowan (1940) taxonomy, we examined the patterns of admixture and potential hybridization among $K = 3$.

In the *STRUCTURE* analysis of $K = 3$, the q -values for 19 individuals (5.47%) were below the 0.90 assignment

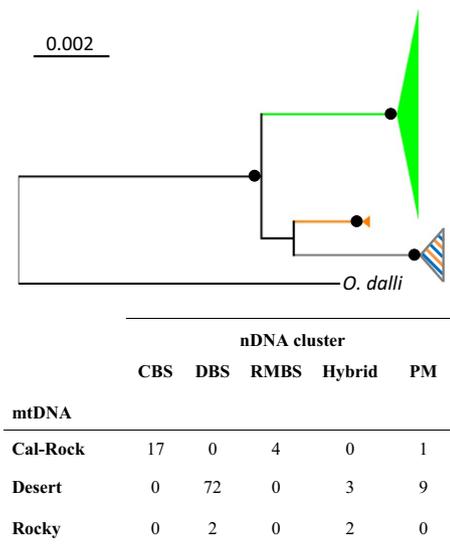


Figure 3 Mitochondrial ND5 gene variation of bighorn sheep (*Ovis canadensis*) in the Great Basin and northern Mojave deserts. Top: Majority-rule consensus phylogram of the Bayesian reconstruction under the HKY + I model of evolution using 110 samples. Black circles at nodes correspond to posterior probabilities (≥ 0.95) from 50,000 post-burn in trees. Bottom: Comparison of mtDNA clade membership with corresponding nDNA *STRUCTURE* cluster assignments ($K = 3$) including hybrids and potentially admixed (PM) individuals.

threshold to any cluster (Fig. 3). Five of these samples had q -values supporting assignment to two clusters with 95% credibility intervals that did not encompass zero (see

Appendix S1) and therefore were characterized as well-supported hybrids. The remaining 14 individuals also had q -values supporting assignment to more than one cluster, but with credibility intervals that encompassed zero, indicating that some searches identified these individuals as pure. We report this latter inconclusive group as ‘potentially admixed’ in anticipation of broader genomic coverage that may provide further insights of genomic affinities.

The five hybrid individuals were spatially distributed in areas that could plausibly experience contact and interbreeding between management units (Fig. 4). Among these, two occurred in the Badlands herd (Unit 74) with a hybrid signature of RMBS-DBS. We identified two well-supported RMBS-DBS hybrids in the dataset, one in the White Pine herd (Unit 131) and the other in the Arrow herd (Unit 244). Unit 131 is managed as DBS, and we recover pure DBS from this herd, but our analyses also uncovered a pure nuclear RMBS. Finally, we document CBS-DBS hybrid ancestry from the Santa Rosas herd (Unit 51). Four of the five well-supported hybrids had maternally inherited mtDNA haplotypes consistent with the local herd.

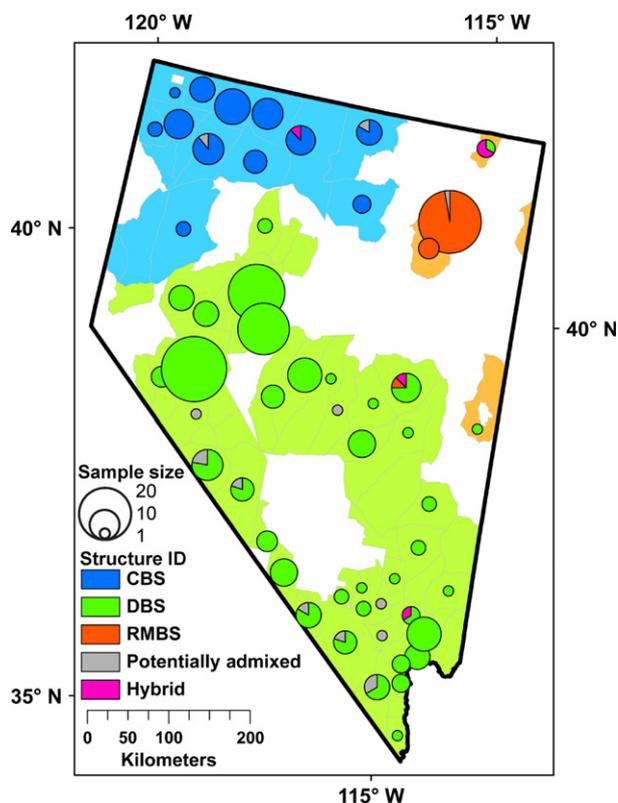


Figure 4 Spatial distribution of genotypic variation for 16 microsatellite loci from 347 samples of bighorn sheep (*Ovis canadensis*) within the Great Basin and northern Mojave deserts. Pie chart sizes show the number of samples from each herd. Pie chart colours correspond to STRUCTURE cluster assignment ($K = 3$). Hybrid and potentially admixed individuals are shown separately according to criteria given in text.

The spatial distribution of the remaining 14 potentially admixed individuals is consistent with plausible areas of contact among genetic clusters and perhaps from groups outside the study area. For example, several individuals with potentially admixed genomes occur along the western portion of the Great Basin and Mojave deserts, near California (Fig. 4). The genomes in these populations may be the result of genetic exchange with bighorn sheep in eastern California. More comprehensive genomic and broader spatial sampling of this system is warranted to further clarify current and historic connectivity.

Niche-based analyses

Ordination

We obtained 26 niche-based variables to explore variation in environmental space (E-space) among scenopoetic variables (Peterson *et al.*, 2011) using three independent PCAs. The dataset was reduced to thirteen variables because of significant autocorrelation.

In comparing areas associated with each of the genetic clusters identified in this study, we found separation in the mean distributions of niche space among each group but with overlap in confidence ellipses (Fig. 5, Table S2). We explored strong loadings > 0.4 for the first three components that accounted for 67% of the variation (Table S2; Figure S3). The first component reflected an elevation-associated relationship where higher elevations and increased summer precipitation contrast with lower annual temperatures. Negative loadings for PC1 included annual and summer precipitation variables (bio12, bio18) and elevation, but positive for mean annual temperature (bio1). The second component loaded negatively for diurnal temperature range (bio2) and isothermality (bio3), reflecting a temperature variation relationship. Finally, axis 3 revealed an association of temperature–precipitation seasonality with positive loading for wet quarter temperature (bio8) and negative loadings for driest quarter temperature (bio9) and precipitation seasonality (bio15).

In the NBSMA versus background PCA, four axes accounted for $> 70\%$ of the variation (Figure S2, Table S3). We explored strong loadings > 0.40 that show, in general, the NBSMA had cooler temperatures and higher moisture and occurred at higher elevations than background samples.

Finally, in comparing areas available to CBS and RMBS in their translocated range in Nevada to those in their source areas, we found significant differences in niche space (Fig. 6). Areas available to translocated bighorn sheep were significantly more xeric as compared with either the Canadian Rockies (British Columbia) or the southern Rocky Mountains (Colorado). We retained the first three components that accounted for $> 80\%$ of the variation and reflected minimal overlap (Table S4). The first component showed a positive relationship between isothermality (bio3) and mean temperature of the wettest quarter (bio8), or a seasonal precipitation association. For the second component, we

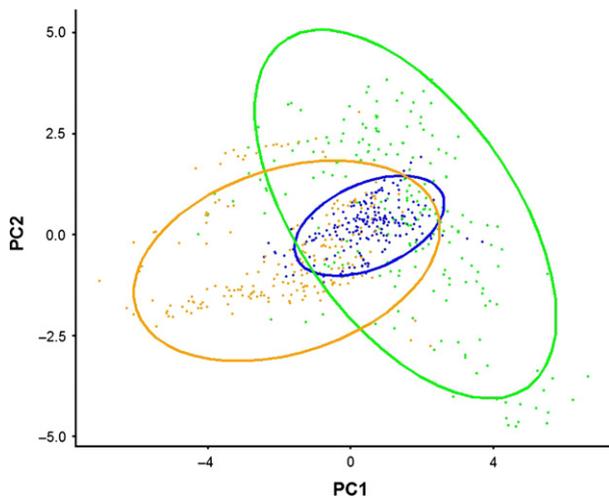


Figure 5 Ecological variation for Herds of translocated bighorn sheep (*Ovis canadensis*) within Nevada. Scatter plot and 75% confidence ellipses of the management unit PCA using 13 variables (Table S2) to explain > 67% of variation from random pseudo-presence samples (200 per unit) for California (blue), desert (green), and Rocky Mountain (orange) bighorn sheep. PC1 reflects an elevation-associated relationship, and PC2 represents a relationship between seasonal variation in temperature and precipitation (see Appendix S1).

observed positive loadings for warm quarter precipitation (bio18) and land cover with negative loadings for mean temperature of the driest quarter (bio9), reflecting a strong relationship among seasonally variable temperature, precipitation and land cover.

DISCUSSION

Repatriation programmes have facilitated the recovery of bighorn sheep (Krausman, 2000) following population losses (Buechner, 1960). From a conservation biology perspective, management action should seek to maintain ecological and evolutionary processes (Moritz, 1999; Crandall *et al.*, 2000; Moritz & Potter, 2013) and consider biogeographic history (Malaney & Cook, 2013). Much of the genetic and niche-based differences we observe are presumably the result of a dynamic history following divergence from *O. dalli* (Rezaei *et al.*, 2010) and diversification that occurred in geographically isolated populations (Loehr *et al.*, 2006). Many organisms (Pearman *et al.*, 2008), including large-bodied mammals (Pease *et al.*, 2009; Richmond *et al.*, 2010; D'Amen *et al.*, 2013), presumably experienced geographic isolation with regional niche adaptation leading to ecogeographic variation (Sobel *et al.*, 2010). Given the magnitude of genetic and niche-based differentiation that appears to exist across the range of bighorn sheep we sampled, translocation efforts need to carefully consider, in tandem, genetic structure (Hedrick, 2013), the scenopoetic niche (Soberón, 2007; Guisan *et al.*, 2013, 2014) and adaptations to local environments (Crandall *et al.*, 2000; Allendorf *et al.*, 2013).

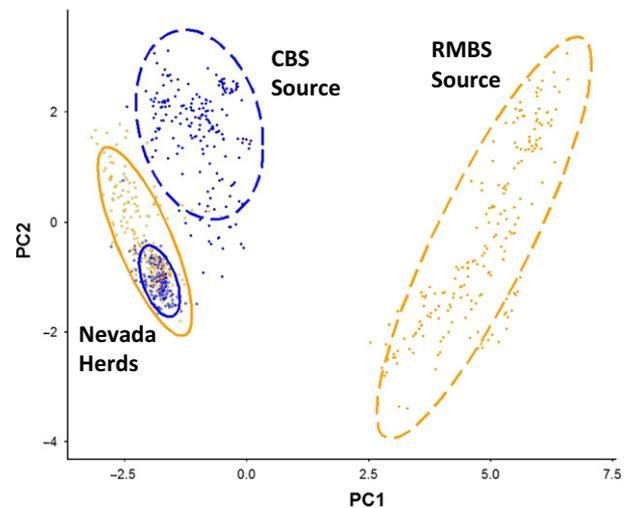


Figure 6 Translocated to the fringe. Scatter plot and 75% confidence ellipses of the first two components that account for over 80% of the variation when comparing source ranges (closed symbols, dashed ellipses) to translocated Herds (NBSMAs; open symbols, solid ellipses) of bighorn sheep (*Ovis canadensis*). The best two predictor variables for PC1 were mean annual precipitation (+) and mean annual temperature (−) that together account for nearly 65% of the variation. The second component reflects an isothermality (+) to land cover relationship (−).

Genetic divergence and niche differences

Neutral microsatellites and mtDNA data reflect a signal of subdivision between boreal-montane (RMBS and CBS)- and desert-montane (DBS)-associated bighorn sheep. Nuclear genetic variation is further subdivided into the boreal-montane-associated sheep, leading to concordance with the three currently recognized management units. Because of their close evolutionary relationship, Wehausen & Ramey (2000) recognized CBS and RMBS as indistinct and synonymized these designations. Our analysis also finds a close evolutionary relationship between CBS and RMBS, but highlights a more complex history for RMBS (Fig. 3). Further, our nDNA analyses reveal subdivision between CBS and RMBS clusters comparable to their differentiation from DBS (Fig. 2). The magnitude of differentiation uncovered between CBS and RMBS in their translocated range warrants further investigation within native ranges. CBS and RMBS may be discrete genetic units with a sharp disjunction at range margins, which would suggest some barrier to gene flow between these units. Alternatively, the genetic units in the Great Basin may be the result of sampling from the ends of a single, diverse taxon exhibiting clinal variation across > 2000 km. Further, genetic differentiation between CBS and RMBS in the translocated range may partly be the result of founder effects that can rapidly augment divergence (Hedrick *et al.*, 2001). Founder events often lead to low diversity, and indeed, we documented low allelic diversity and heterozygosity in our sample of CBS and RMBS compared to DBS (Table 1). However, we lack a comparison of diversity to the native range for CBS and

RMBS, and broader sampling across the native ranges, with special emphasis in areas of potential contact, will allow better resolution of these alternatives.

We observed few niche-based differences within the Great Basin among our observed genetic clusters (Fig. 5) with the best prediction along an elevational gradient (PC1), followed by temperature and precipitation seasonality (PC2 & PC3; Table S2). A direct comparison of loadings for component variables revealed that RMBS management areas occur at higher elevations are generally cooler and more mesic and tend to be less seasonally variable. Conversely, DBS areas have the lowest elevations, with comparatively warmer and more xeric conditions, but experience the highest seasonal variability, and CBS areas were intermediate along these axes. These broad niche-based associations are consistent with the known ecology of desert-montane and boreal-montane sheep (Shackleton, 1985) and are the result of translocations that targeted these distinct regions within the Great Basin. Nonetheless, our analysis suggests that management areas targeted for one subspecies contain environmental niche space that could potentially support other bighorn subspecies (Fig. 5). Consequently, the spatial and environmental proximity among genetic units may provide opportunities for admixture.

Admixture

Our analyses revealed genetic divergences among bighorn sheep in Nevada that likely arose through ancestral geographic subdivision among these units. Nonetheless, at the margins of the translocated ranges, these distinct units now come into close proximity, creating the potential for spatial overlap and interbreeding (Fig. 4). For example, within the White Pine herd (current mountains), we detected pure RMBS, pure DBS and an admixed individual (Fig. 4). This unit is managed as DBS, so the presence of RMBS genotypes was unexpected. In far northern Nevada, we sampled three individuals from the Badlands herd, a location stocked with

RMBS. From this site, we document two admixed individuals (RMBS × DBS) and the third showed a pure DBS genotype, but we failed to detect any pure RMBS. It remains unclear whether the signal of DBS in the Badlands herd is the product of historic genetic variation (perhaps from a remnant herd), long-distance dispersal (although the nearest DBS herd is > 250 km away) or other unrecorded events. Likewise, the unexpected presence of DBS genotypes in Great Basin National Park could be the result of remnant variation or recent dispersal from nearby DBS Herds. The unexpected RMBS in the White Pine herd is likely due to recent dispersal considering the close proximity to RMBS Herds. These spatially unexpected individuals had mtDNA haplotypes consistent with their nuclear genomes. Conversely, nearly all hybrids had mtDNA haplotypes consistent with their collection site, indicating that early generation hybrids may often result from rare migrant males mating with resident females.

To our knowledge, we are the first to report admixture between these groups, and while we have clear evidence of hybridization, identifying the frequency and spatial extent of admixture and introgression will require additional sampling. Knowing the potential for admixture, the environmental and demographic conditions promoting it, and the distribution of extant admixed individuals is critical for proper management.

Translocated to the fringe

Our analyses show that areas available to boreal-montane bighorn sheep (CBS and RMBS) in their translocated range in the Great Basin are characterized by environmental conditions that significantly differ from source areas (Fig. 6). Because our analyses are predicated on available areas rather than precise measurements of actual habitat use (*e.g.* from radiotelemetry), it may be that animals in the translocated ranges are using subsets of available conditions most similar to source areas, thereby minimizing the environmental mismatch they experience. Even if translocated animals experience environmental conditions significantly distinct from source areas, there may be minimal fitness consequences if these animals have a wider 'tolerance' niche (Sax *et al.*, 2013) than expected from their realized niche (Soberón & Peterson, 2005; Guisan *et al.*, 2014). Individual populations of bighorn sheep are known to adjust to new conditions after translocation by altering the timing and synchrony of parturition, which augments population persistence (Whiting *et al.*, 2011, 2012). High phenotypic plasticity may explain why some translocated bighorn sheep persist and even thrive (NDOW, 2001; Rominger *et al.*, 2004; Epps *et al.*, 2005; Wiedmann & Sargeant, 2014) and may ultimately be the result of an evolutionary past that necessitated rapid acclimation to changing conditions (Hof *et al.*, 2011).

An alternative perspective is that translocated populations may be under physiological stress if they reside outside native environmental conditions. Wiedmann & Sargeant (2014) found dramatic differences in recruitment between distinct ecotypic stocks translocated to North Dakota,

Table 1 Mean and standard error (below and italic) of diversity metrics for 16 microsatellite loci from 328 individuals (hybrid and potentially admixed individuals excluded) across three bighorn sheep (*Ovis canadensis*) management units within the Great Basin and northern Mojave deserts. Metrics include number of alleles (N_A), effective alleles (N_E), plus observed (H_O), expected (H_E) and unbiased expected (U_{H_E}) heterozygosity.

	N	N_A	N_E	H_O	H_E	U_{H_E}
CBS	68	4.500	2.123	0.406	0.460	0.464
		<i>0.387</i>	<i>0.217</i>	<i>0.059</i>	<i>0.049</i>	<i>0.049</i>
DBS	219	7.875	3.863	0.573	0.677	0.668
		<i>0.865</i>	<i>0.455</i>	<i>0.047</i>	<i>0.052</i>	<i>0.052</i>
RMBS	41	4.750	2.745	0.491	0.570	0.577
		<i>0.382</i>	<i>0.291</i>	<i>0.044</i>	<i>0.044</i>	<i>0.045</i>
Total	328	5.708	2.910	0.490	0.566	0.570
		<i>0.402</i>	<i>0.217</i>	<i>0.030</i>	<i>0.030</i>	<i>0.030</i>

suggesting that adaptation to local environmental conditions is a strong determinant of post-translocation population persistence. If mismatch with local environmental conditions leads to greater physiological stress in translocated populations, they may be more susceptible to other stressors including disease (Besser *et al.*, 2008, 2012; Wehausen *et al.*, 2011) and predation (Wehausen, 1996; Rominger *et al.*, 2004). Although synergisms among multiple threats or stressors in fringe populations are poorly understood (Festa-Bianchet *et al.*, 2006), minimizing niche-based mismatch could enhance translocation success (Guisan *et al.*, 2013).

CONCLUSIONS

By integrating analyses, we developed a more comprehensive perspective of the species–environment relationship and show that translocations are moving bighorn sheep to disparate environmental conditions and likely contributing to admixture of divergent genomes. Bighorn sheep are among the most iconic species in North America, and one of the best examples of how bold management has facilitated the persistence of an imperilled species. However, a better understanding of how previous translocation efforts have altered genomes and re-distributed populations, especially to novel environmental conditions, is important for long-term sustainability. That these populations persist in fringe conditions may mean that bighorn sheep are resilient to a broad spectrum of environmental conditions, or conversely, more susceptible to other stressors. More broadly, our study shows that much can be learned from past conservation and management activities, especially translocation and repatriation programmes. A clear understanding of infraspecific genetic variation, niche-based differences and the ramifications of various translocation strategies will be important for conservation of many species, especially when considering rapid environmental changes on the horizon.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1

Table S1 Chi-square (χ^2) goodness-of-fit tests for the deviation from Hardy–Weinberg Equilibrium (HWE) from 16 microsatellite loci, across 328 samples, for three management units of bighorn sheep (*Ovis canadensis*), and three individual Herds. Significance (asterisk) was adjusted for multiple tests by Dunn–Šidák correction ($N = 48$; $P < 0.001$).

Table S2 Management Unit PCA (see Fig 5a) loadings from 600 (200 per unit – CBS, DBS, RMBS) pseudo-presence samples of bighorn sheep (*Ovis canadensis*) within NBSMAs (see Figs 1 and 5b).

Table S3 Nevada Bighorn Sheep Management Areas (NBHMSA, $N = 600$) and random background samples ($N = 600$) PCA results for 13 niche variables (see Figure S2).

Table S4 Translocated bighorn sheep (*Ovis canadensis*) and source Herds (British Columbia and Colorado) PCA eigenvectors for 13 niche variables (see Fig. 6).

Table S5 Multiplex PCR design with fluorescently labeled microsatellite primers used for genotyping bighorn sheep ($N = 328$) in Nevada with locus-specific number of observed alleles (k) and range, plus observed (H_o) and expected (H_e) heterozygosity.

Figure S1 Comparison of PCoA scatter plots of putative identifications (based on management units) and STRUCTURE assignments for $K = 2$ and $K = 3$ of bighorn sheep (*Ovis canadensis*) in the Great Basin and northern Mojave Deserts.

Figure S2 Test for spatial autocorrelation.

Data S1 Supplementary Methods.

BIOSKETCH

Our team has a research focus on the population and evolutionary genetics of western North American vertebrates and interested in integrated approaches using genetic and niche-based tests to provide novel perspectives for conservation and management.

Author contributions: M.C., P.W., and J.W. collected the samples, J.L.M. and C.R.F. conducted the lab work, all contributed to conceptualizing the research ideas and writing the manuscript.

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