## AN ABSTRACT OF THE DISSERTATION OF

<u>Tyler G. Creech</u> for the degree of <u>Doctor of Philosophy</u> in <u>Wildlife Science</u> presented on <u>January 25, 2016.</u>

Title: Landscape-Level Approaches to Desert Bighorn Sheep (*Ovis canadensis nelsoni*) Conservation in a Changing Environment.

Abstract approved: \_\_\_\_\_

Clinton W. Epps

Landscape characteristics can strongly influence demographic and genetic processes in wildlife populations. Climate change and human land use are causing many landscapes to change rapidly, and the effects on wildlife populations must be understood to properly manage these threats and design effective conservation strategies. In this dissertation, I explored the implications of landscape heterogeneity for desert bighorn sheep (*Ovis canadensis nelsoni*), an ecologically and culturally important ungulate species in the southwestern United States, and demonstrated new approaches that can be applied to landscape-level conservation of many wildlife species in changing landscapes. This research focused on populations within and surrounding U.S. national parks, comprising a large portion of the desert bighorn sheep's geographic range, and utilized a genetic dataset including > 1,600 individuals that was developed during this and previous projects.

Landscape resistance models have been used extensively to predict potential linkages among fragmented wildlife populations, including desert bighorn sheep, but have rarely been used to guide systematic decision-making such as prioritizing conservation actions to maximize regional connectivity. In Chapter 1, I combined network theory and landscape resistance modeling to prioritize management for connectivity, including protection and restoration of dispersal corridors and habitat patches, in a desert bighorn sheep metapopulation in the Mojave Desert. I constructed network models of genetic connectivity (potential for gene flow) and demographic connectivity (potential for colonization of empty habitat patches). I found that the type of connectivity and the network metric used to quantify had substantial effects on prioritization results; however, I was able to identify high-priority habitat patches and corridors that were highly ranked across all combinations of the above factors.

Potential diet quality varies across landscapes and through time for desert bighorn sheep and other ungulates, but is difficult to measure at fine spatial and temporal resolution using traditional field-based methods. The remotely sensed vegetation index NDVI can potentially overcome these limitations, but its relationship to diet quality has never been empirically validated for desert herbivores. In Chapter 2, I examined how strongly NDVI was associated with diet quality of desert bighorn sheep in the Mojave Desert using fecal nitrogen data from multiple years and populations, and considered the effects of temporal resolution, geographic variability, and NDVI spatial summary statistic. I found that NDVI was more reliably associated with diet quality over the entire growing season than with instantaneous diet quality for a population, and was positively associated with population genetic diversity (a proxy for long-term diet quality). Although NDVI was a useful diet quality indicator for Mojave Desert bighorn sheep, my analysis suggested that it may be unreliable if satellite data are too spatially coarse to detect microhabitats providing high-quality forage, or if diet is strongly influenced by forage items that are weakly correlated with landscape greenness.

Landscape genetic studies typically rely on neutral genetic markers to explore gene flow and genetic variation, but the potential for species to adapt to changing landscapes depends on how natural selection influences adaptive genetic variation. In Chapter 3, I optimized landscape resistance models for desert bighorn sheep in three regions with different landscape characteristics, and then used genetic simulations incorporating natural selection to determine how the spread of adaptive variation is influenced by differences among landscapes. Optimized landscape resistance models differed between regions but slope, presence of water barriers, and major roads had the greatest impacts on gene flow. Differences among landscapes strongly influenced the spread of adaptive genetic variation, with faster spread in landscapes with more continuously distributed habitat and when a pre-existing allele (i.e., standing genetic variation) rather than a novel allele (i.e., mutation) served as the source of adaptive genetic variation.

Climate change presents a substantial threat to desert bighorn sheep and wildlife worldwide, and adaptation may be required to persist in novel environmental conditions. Knowledge of how adaptive capacity - the potential to cope with climate change by persisting *in situ* or moving to more suitable ranges or microhabitats - varies across populations is needed to establish conservation priorities for minimizing climate change impacts to individual species. In Chapter 4, I explored variation in the evolutionary component of adaptive capacity for 62 desert bighorn sheep populations on and near U.S. national parks. I measured adaptive capacity of populations as a function of two factors that are strongly associated with the potential for evolutionary adaptation, genetic diversity and connectivity (estimated using a landscape resistance model from Chapter 3). Genetic diversity and connectivity were highly variable across regions and populations. I identified populations with high adaptive capacity that could serve as genetic refugia from climate change impacts (e.g., those in Death Valley and Grand Canyon National Parks), but also populations with low adaptive capacity that may require conservation actions to improve their potential for adaptation (e.g., those in eastern Utah and the southern Mojave Desert). Genetic structure analyses suggested that populations in eastern Utah were genetically distinct from the rest of the study area, likely resulting from restricted gene flow following regional population extinctions.

This dissertation highlighted the effects of landscape heterogeneity on genetic and demographic processes in desert bighorn sheep populations. Collectively, the information in these chapters should help guide management of desert bighorn sheep in the face of climate change and human land use. The landscape-level approaches demonstrated here may be useful for managing many other wildlife species. ©Copyright by Tyler G. Creech January 25, 2016 All Rights Reserved

## Landscape-Level Approaches to Desert Bighorn Sheep (*Ovis canadensis nelsoni*) Conservation in a Changing Environment

by Tyler G. Creech

## A DISSERTATION

submitted to

Oregon State University

in partial fulfillment of the requirements for the degree of

Doctor of Philosophy

Presented January 25, 2016 Commencement June 2016 Doctor of Philosophy dissertation of Tyler G. Creech presented on January 25, 2016

APPROVED:

Major Professor, representing Wildlife Science

Head of the Department of Fisheries and Wildlife

Dean of the Graduate School

I understand that my dissertation will become part of the permanent collection of Oregon State University libraries. My signature below authorizes release of my dissertation to any reader upon request.

Tyler G. Creech, Author

## ACKNOWLEDGMENTS

This work would not have been possible without the support and contributions of many people. First and foremost, I would like to thank my advisor, Clint Epps, who guided me through my PhD with skill and kindness while demonstrating what can be achieved with hard work and dedication. I am grateful to my committee members – Erin Landguth, Lisa Ganio, Matt Betts, and Rob Wheatcroft – for their input and assistance during my time at OSU. Ryan Monello was a tireless advocate for this project and was instrumental in designing the research and ensuring financial and logistical support. John Wehausen shared his considerable knowledge of bighorn sheep, as well as hard-earned genetic and diet-quality data, to improve many aspects of this dissertation. Jef Jaeger and Kathy Longshore kindly provided genetic data that allowed me to expand the scope of Chapters 3 and 4. Bill Monahan provided helpful advice on climate models. Numerous individuals from the National Park Service offered their time and expertise to make the field sampling for this study a success, including Scott Ratchford, Brandon Holton, Bill Sloan, Jordan Spaak, Lonnie Pilkington, Stacy Holt, Linda Manning, Gary Lenhart, Mark Miller, and Claire Crow. I am deeply indebted to Rachel Crowhurst, who genotyped thousands of samples with the help of Clark Peterson and Madison Corbin, and without whom this dissertation simply would not have been possible. Many current and past members of the Epps lab provided useful feedback and much-needed comradery while working towards my PhD; thanks especially to Katie Moriarty, Doni Schwalm, Rob Spaan, Brandon Nickerson, Jessica Castillo, and Mike Buchalski. Lastly, I would like to express my profound gratitude to my family, particularly my wife Sarah, for their unwavering support. I could not have made it through the challenges of the last five years without them.

## CONTRIBUTION OF AUTHORS

Tyler G. Creech collected genetic samples, designed studies, analyzed data, and wrote manuscripts. Clinton W. Epps obtained funding for the project, collected genetic samples, shared genetic and diet quality data from previous projects, and provided guidance on study design, data analysis and interpretation, and writing of manuscripts. Ryan J. Monello obtained funding for the project, arranged and conducted field work, and edited manuscripts. John D. Wehausen shared genetic and diet quality data from previous projects, provided guidance on data analysis and interpretation, and edited manuscripts. Rachel S. Crowhurst genotyped genetic samples for Chapters 3 and 4. Brandon Holton and William B. Sloan collected genetic data from previous projects. Erin L. Landguth assisted with genetic simulations and manuscript edits for Chapter 3.

## TABLE OF CONTENTS

General Introduction1
Literature Cited
Chapter 1: Using network theory to prioritize management in a desert bighorn sheep metapopulation
Abstract9
Introduction10
Methods13
Study area13
Genetic-based connectivity models
Network models15
Evaluating contribution of individual patches and corridors to connectivity
Sensitivity analysis18
Testing ecological relevance of network metrics
Results19
Discussion
Analytical limitations22
Recommended actions in the Mojave Desert region23
Applying the network approach in conservation25
Acknowledgments
Literature Cited
Tables and Figures

Chapter 2: Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI
Abstract
Introduction
Methods41
Study area41
NDVI data42
Fecal nitrogen data43
Relationship between NDVI and fecal nitrogen44
Characteristics of FN and NDVI curves46
Relationship between NDVI and genetic diversity46
Results48
Sample-level FN versus NDVI
Season-level FN versus NDVI48
Characteristics of FN and NDVI curves49
Genetic diversity versus NDVI49
Discussion
Variation among habitat patches50
Effects of temporal resolution51
Drivers of NDVI and FN51
Summarizing NDVI within a habitat patch
NDVI and genetic diversity53

Saturation effect of NDVI53
Limitations54
Conclusions
Acknowledgments
Literature Cited
Tables and Figures61
Chapter 3: Simulating the spread of selection-driven genotypes using landscape resistance models for desert bighorn sheep
Abstract
Introduction69
Methods72
Study area72
Genetic data73
Genetic distances74
Landscape variables75
Candidate univariate surfaces76
Cost distances77
Resistance surface optimization77
Simulation of adaptive allele spread79
Results
Genetic data82
Univariate optimization82

Multivariate optimization83
Simulation83
Discussion
Resistance modeling85
Simulating selection
Implications for conservation and management90
Applications91
Acknowledgments92
Literature Cited92
Tables and Figures
Chapter 4: Genetic structure and adaptive capacity of desert bighorn sheep in national parks of the southwest United States
Abstract104
Introduction105
Methods109
Study area109
Genetic sampling and genotyping methods110
Defining populations and habitat patches110
Genetic structure
Genetic diversity
Connectivity113
Adaptive capacity115

Results115
Genetic structure
Genetic diversity
Connectivity117
Adaptive capacity118
Discussion118
Genetic structure and diversity
Geographic variation in adaptive capacity12
Management actions to maximize adaptive capacity
The role of national parks
Improving adaptive capacity estimates
From adaptive capacity to climate change vulnerability
Acknowledgments128
Literature Cited
Tables and Figures  137
General Conclusion147
Literature Cited
Bibliography150
Appendices169

## LIST OF FIGURES

<u>Figure</u> <u>Page</u>
1.1. Desert bighorn sheep habitat patches in the Mojave Desert region considered in Chapter 1
1.2. Prioritization of patch and edge protection according to network type and network metric
2.1. Bighorn sheep populations and associated habitat patches in Chapter 262
2.2. Median NDVI and fecal nitrogen for the Marble Mountains and Old Dad Peak populations
2.3. Relationship between fecal nitrogen and NDVI at the sample level for five bighorn sheep populations from 2000-2011
2.4. Relationship between integrated fecal nitrogen and log of integrated NDVI during the OctJune growing season for the Marble Mountains and Old Dad Peak habitat patches from 2001-2011
2.5. Mean monthly percentages of total growing season area-under-curve (INDVI or IFN) in the Marble Mountains and Old Dad Peak patches
2.6. Relationship between genetic diversity and NDVI for 22 populations in the Mojave Desert
3.1. Study regions and sampling location for Chapter 3100
3.2. Simulated change in adaptive allele frequency through time under the novel allele scenario
3.3. Simulated change in adaptive allele frequency through time under the pre-existing allele scenario
3.4. Proportion of Monte Carlo replicates in which adaptive allele is present in each individual location in three regions
4.1. Map of study area including ten national parks and 62 desert bighorn sheep populations included in analysis
4.2. Cluster assignment probabilities from STRUCTURE analysis for 62 desert bighorn sheep populations

# LIST OF FIGURES (Continued)

<u>Figure</u> <u>Page</u>
4.3. Scatterplots of first two principal component axes from DAPC analyses for 62 desert bighorn sheep populations
4.4. Population assignments to clusters from DAPC analysis for 62 desert bighorn sheep populations
4.5. Comparison of genetic diversity, connectivity, and adaptive capacity across regions and between populations within versus outside national parks
4.6. Adaptive capacity of 62 desert bighorn sheep populations as a function of genetic diversity and connectivity
B.1. Histogram of effective distances of known ewe dispersal events
B.2. Estimated relationships between Nm and effective distance
B.3. Example of a redundant edge in the Mojave bighorn network
C.1. Sensitivity of prioritization results to error in estimated ED <sub>MAX</sub> for males and females
C.2. Proportion of original feature set remaining in new feature set as a function of ED <sub>MAX</sub> in genetic demographic networks
C.3. Proportion of new feature set absent from original feature set as a function of $ED_{MAX}$ in genetic and demographic networks
F.1. Degree distribution of the observed network versus the average Erdos-Renyi network of the same size for genetic and demographic networks
G.1. Prioritization of corridor restoration in the genetic network as ranked by ECP and MWC
G.2. Prioritization of corridor restoration in the demographic network as ranked by ECP and MWC
G.3. Prioritization of patch restoration in the genetic network as ranked by ECP and MWC
G.4. Prioritization of patch restoration in the demographic network as ranked by ECP and MWC

# LIST OF FIGURES (Continued)

<u>Figure</u> <u>Page</u>
H.1. Availability of fecal nitrogen data for five bighorn sheep habitat patches in the Mojave Desert
H.2. Distribution of number of fecal pellet groups composited per fecal nitrogen observation
H.3. Comparison of the relationship between fecal nitrogen and untransformed or log- transformed NDVI summary statistics for the Marble Mountains population201
H.4. Comparison of the relationship between fecal nitrogen and untransformed or log- transformed NDVI summary statistics for the Old Dad Peak population
H.5. Time series (2000-2011) of median NDVI, 90th percentile NDVI, and maximum NDVI for five habitat patches used in fecal nitrogen analysis
H.6. Distribution of NDVI values in one growing season image and one non-growing season image for five habitat patches used in fecal nitrogen analysis
H.7. Relationship between fecal nitrogen and NDVI at the sample level for five populations
H.8. Time series (2000-2011) of median NDVI for five patches used in fecal nitrogen analysis
H.9. Relationships between integrated fecal nitrogen or integrated NDVI and peak height or peak width during 2001-2011 growing seasons in the Marble Mountains and Old Dad Peak patches
H.10. Relationship between genetic diversity and NDVI for 22 Mojave Desert populations after accounting for population connectivity
K.1. Example monotonic relationships between resistance and a landscape variable217
K.2. Example Gaussian relationships between resistance and a landscape variable217
L.1. Likelihood estimate for each value of K from STRUCTURE analysis for 62 desert bighorn sheep populations
L.2. Rate of change in the likelihood function from STRUCTURE analysis for 62 desert bighorn sheep populations

# LIST OF FIGURES (Continued)

<u>Figure</u> <u>P</u>	'age
L.3. Individual cluster assignment probabilities from STRUCTURE analysis for 62 de bighorn sheep populations	esert .222
N.1. Relationship between genetic diversity and connectivity of 62 desert bighorn she populations	ер .225

## LIST OF TABLES

<u>Table</u> <u>Page</u>
1.1. Correlation of prioritization results between networks and between metrics for different management actions
1.2. High priority patches and corridors for protection or restoration in genetic and demographic networks
1.3. Effects of four multi-part conservation scenarios on connectivity of genetic and demographic networks
2.1. Effects of peak height and peak width of fecal nitrogen and NDVI curves on integrated fecal nitrogen and integrated NDVI
2.2. Models of relationship between genetic diversity and long-term NDVI for 22 bighorn sheep populations in the Mojave Desert
3.1. Optimized univariate resistance models for three regions
3.2. Optimized multivariate resistance models for three regions
4.1. Characteristics of 62 desert bighorn sheep populations in the study area, including translocation history, proximity to national parks, genetic diversity, connectivity, and adaptive capacity
A.1. Names and abbreviations of bighorn habitat patches included in Chapter 1170
E.1. Linear regression of genetic diversity on patch-level analogs of network metrics used to describe connectivity for desert bighorn sheep populations in the Mojave Desert182
G.1. Prioritization results for patch protection in genetic and demographic networks based on ECP and MWC
G.2. Prioritization results for corridor protection in genetic and demographic networks based on ECP and MWC
G.3. Prioritization results for patch restoration in genetic and demographic networks based on ECP and MWC
G.4. Prioritization results for corridor restoration in genetic and demographic networks based on ECP and MWC
H.1. Location, size, and sampling intensity for habitat patches included in Chapter 2197

# LIST OF TABLES (Continued)

<u>Table</u> <u>Page</u>
H.2. Pearson's correlation coefficient between connectivity metrics and genetic diversity indices
H.3. Pearson correlation coefficient between fecal nitrogen and each of three summary statistics of NDVI
H.4. Models of relationship between genetic diversity and long-term NDVI for 22 bighorn sheep populations with Gaussian spatial correlation structure
I.1. Microsatellite locus information
J.1. Geospatial data sources for landscape variables
K.1. Alternative resistance curves for continuous landscape variables
K.2. Alternative resistance ratios for categorical landscape variables

Appendix	Page
A. Patch names and abbreviations for Chapter 1	170
B. Constructing genetic and demographic networks	171
C. Sensitivity analysis	177
D. Network metrics	180
E. Testing relevance of network metrics	181
F. Network properties	184
G. Prioritization results	186
H. Supplementary material for Chapter 2	195
I. Genetic laboratory methods	209
J. Geospatial data for Chapter 3	215
K. Landscape resistance models for Chapter 3	216
L. Genetic structure analysis	220
M. Landscape resistance model for Chapter 4	223
N. Relationship between genetic diversity and connectivity	224

## LIST OF APPENDICES

## GENERAL INTRODUCTION

Conservation and management of wildlife populations has undergone a transformation since the emergence of the field of landscape ecology several decades ago. Landscape ecology emphasizes the interaction between spatial patterns on ecological processes at broader extents than have traditionally been considered in ecological studies (Turner et al. 2001), and has produced some key insights into the ways that landscape-level patterns affect demographic processes in wild populations (Bissonette 2012). For instance, wildlife managers now widely recognize the effects of habitat loss and fragmentation (Saunders et al. 1991), the influence of spatial variation in habitat quality on demographics (Pulliam 1988), and the role that the matrix between habitat patches can play in determining dispersal and gene flow (Gustafson and Gardner 1996; Ricketts 2001). Understanding the influences of landscape characteristics on wildlife populations has taken on new urgency in light of accelerating habitat loss, fragmentation, and climate change.

This dissertation explores the effects and implications of landscape heterogeneity for desert bighorn sheep (Ovis canadensis nelsoni), with the primary goal of improving our ability to effectively manage and conserve bighorn populations in changing environments. The desert bighorn sheep is one of three currently recognized subspecies of North American bighorn sheep (Wehausen and Ramey 2000), with approximately 20,000 individuals currently ranging across the southwestern United States and northern Mexico in arid, rugged environments to which they are adapted (Krausman et al. 1999). Bighorn sheep are habitat specialists that require steeply sloped terrain with good visibility to escape predation, as well as adequate forage and access to reliable surface water (Risenhoover and Bailey 1985). Across much of their range, this habitat is distributed in discrete and relatively isolated patches (Krausman et al. 1999). Desert bighorn sheep were much more abundant prior to European settlement, with total population estimates in the hundreds of thousands, but were extirpated from many areas between the late 1800s and the 1940s as a result of habitat conversion, mining impacts, unregulated harvest, and livestock-borne diseases (Singer and Gudorf 1999). Some of the best remaining habitat occurs on lands administered by the National Park Service in

southern California, southern Nevada, northern Arizona, and southern Utah; populations occupying these areas, including ten national parks, are the focus of the research presented in this dissertation.

Landscapes occupied by desert bighorn sheep have experienced major changes over the last century. For instance, a recent study of landscape changes since 1900 found substantial increases in housing density and non-native species for national parks in the southwest U.S., as well as increased temperature and decreased moisture index (Hansen et al. 2013). Negative impacts of anthropogenic barriers such as interstate highways on genetic diversity of bighorn sheep have been documented (Epps et al. 2005), as have changes in behavior, movement, and habitat use in response to human activity and development (Leslie and Douglas 1980; Papouchis et al. 2001; Rubin et al. 2002). Projected changes in climate for the next century are likely to further threaten desert bighorn sheep populations. Climate models consistently predict increases in temperature across the subspecies' range of approximately 2 - 5 °C by 2100 (Bachelet et al. 2016; Garfin et al. 2014; Hansen et al. 2013). The predicted magnitude and direction of precipitation change vary considerably among climate models and by location, but the southwest U.S. as a region is predicted to be more arid and have reduced surface water availability in the future (Seager et al. 2007; Seager et al. 2013). The dual threats of climate change and human land use necessitate a proactive, landscape-based approach to desert bighorn sheep conservation. A primary tool in this dissertation research is the most extensive genetic dataset to date for desert bighorn sheep, which includes > 1,600genotyped individuals and was developed during this dissertation and several previous research projects. While the four chapters of this dissertation focus on desert bighorn sheep populations, a secondary goal of this research is to demonstrate new approaches that can be applied to landscape-level conservation of many wildlife species facing similar threats.

The importance of connectivity has been widely recognized for bighorn sheep (Bleich et al. 1996; Epps et al. 2005) and for wildlife populations in general (Bennett 1999). Ecological and demographic processes including gene flow, migration, dispersal from natal ranges, range shifts in response to climate change, and metapopulation dynamics are dependent on connectivity (Crooks and Sanjayan 2006). Landscape resistance models, often developed using genetic data, have become a primary tool for understanding and managing connectivity; for instance, such models are frequently used to evaluate or map prospective dispersal corridors (Cushman et al. 2010; Wasserman et al. 2012). However, landscape resistance models alone do not provide guidance on the relative importance of particular landscape elements (e.g., dispersal corridors and habitat patches) to connectivity at broad scales, such as metapopulations (Keller et al. 2015). This is a critical limitation to efforts to prioritize management actions to maintain or restore connectivity. In Chapter 1, I address this limitation for a metapopulation of desert bighorn sheep in the Mojave Desert by using landscape resistance models to determine which habitat patches are connected by dispersal, then applying network theory to quantify the contributions of individual patches and dispersal corridors to overall connectivity. I establish priorities for protection or restoration of patches and corridors on the basis of their effects on the potential for gene flow and recolonization of empty habitat at the metapopulation level.

Heterogeneous environments influence more than just the connectivity of habitat patches; differences in the characteristics of habitat patches themselves, such as the availability of resources, also influence wildlife populations. For ungulates like desert bighorn sheep, the availability and nutrient content of forage plants can be highly variable in both space and time, creating variation in diet quality (Albon and Langvatn 1992; Festa-Bianchet 1988; McNaughton 1990). Diet quality strongly influences ungulate population dynamics (Parker et al. 2009) but has traditionally been difficult to measure over broad extents at sufficient temporal and spatial resolution using field-based methods. To circumvent this problem, remotely-sensed vegetation indices are increasingly being used to represent potential ungulate diet quality (Boone et al. 2006; Pettorelli et al. 2007; Ryan et al. 2012), but this approach often relies on untested assumptions about the relationship between the landscape "greenness" measured by satellites and the diet quality experienced by populations inhabiting the landscape. In Chapter 2, I use a longterm diet quality dataset for desert bighorn sheep populations in the Mojave Desert to directly test the relationship between diet quality and the Normalized Difference Vegetation Index (NDVI). I examine the effects of temporal resolution and geographic variability on this relationship, and determine conditions under which NDVI can reliably

predict diet quality for desert bighorn sheep, as well as conditions under which NDVI is likely to fail as a diet quality indicator for bighorn and many other wildlife species.

Landscape genetic approaches in particular have greatly enhanced our understanding of landscape effects on wildlife populations. Landscape genetics combines aspects of population genetics, landscape ecology, and spatial statistics and seeks to understand how genetic variation and gene flow are affected by landscape variables (Manel et al. 2003). For desert bighorn sheep, landscape genetic studies in the Mojave Desert region have quantified the effects of slope and anthropogenic barriers (e.g., interstate highways, urban areas, aqueducts) on gene flow, allowing us to predict which populations are connected by dispersal and the most likely locations of corridors used by dispersing individuals (Epps et al. 2005; Epps et al. 2007). These studies and the vast majority of landscape genetic studies are based on neutral genetic markers because they provide unbiased estimates of gene flow (Holderegger et al. 2006). However, many questions about the effects of landscape characteristics on wildlife populations concern adaptive genetic variation, which is the ultimate driver of evolutionary potential. Desert bighorn sheep provide an interesting test case for examining landscape influences on adaptive genetic variation because key landscape characteristics including the distribution of habitat and the presence of natural and anthropogenic barriers to dispersal vary across their range. In Chapter 3, I use genetic data to develop landscape resistance surfaces independently for three regions, then simulate the spread of an adaptive genetic variation in each region based on gene flow over 100 years across these resistance surfaces. In doing so, I demonstrate an approach with broad conservation applications that can facilitate comparisons within and between landscapes of the potential for spread of beneficial genes.

Adaptive genetic variation is especially relevant to our understanding of species' responses to climate change, as evolutionary adaptation could be an important coping mechanism for species experiencing novel climatic conditions (Skelly et al. 2007). Some species will likely be able to adjust their spatial distributions to track shifting bioclimatic envelopes, but in situ adaptation could be critical for habitat specialists and species with limited dispersal ability or highly fragmented habitat that prevents range shifts (Schloss et al. 2012; Warren et al. 2001). Evolution via natural selection is one mechanism by which

adaptation can occur (Hoffmann and Sgro 2011; Nicotra et al. 2015), and knowledge of how the potential for evolutionary adaptation varies among populations within the ranges of individual species is needed to establish conservation priorities for minimizing climate change impacts. I address this need for desert bighorn sheep in Chapter 4 by quantifying two key factors that influence evolutionary potential – genetic diversity and connectivity – for 62 populations spanning a major portion of the subspecies range. I explore the genetic structure of populations, compare adaptive capacity of populations on the basis of genetic diversity and connectivity, and identify "genetic refugia" that are most likely to successfully mount evolutionary responses to climate change. The results of Chapter 4 should help the National Park Service and other natural resource agencies to proactively manage climate change impacts to desert bighorn sheep at the landscape scale.

Desert bighorn sheep, like many wildlife species, face an uncertain future in which climate change and human land use will present substantial challenges. This dissertation examines some of the ways that landscape heterogeneity influences desert bighorn sheep, and demonstrates new approaches that could allow us to better incorporate these landscape influences into conservation planning. Ultimately, I hope that this research can contribute, however modestly, to preserving a unique and iconic subspecies.

#### LITERATURE CITED

- Albon S, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65(3):502-513
- Bachelet D, Ferschweiler K, Sheehan T, Strittholt J (2016) Climate change effects on southern California deserts. Journal of Arid Environments 127:17-29
- Bennett AF (1999) Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland and Cambridge, UK
- Bissonette JA (2012) Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer Science+Business Media, New York
- Bleich VC, Wehausen JD, Ramey II RR, Rechel JL (1996) Metapopulation theory and mountain sheep: implications for conservation. In: McCullough DR (ed), Metapopulations and Wildlife Conservation. Island Press, Covelo, CA

Boone RB, Thirgood SJ, Hopcraft JGC (2006) Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87(8):1987-1994

- Crooks KR, Sanjayan MA (2006) Connectivity Conservation. Cambridge University Press, Cambridge, UK
- Cushman SA, Chase M, Griffin C (2010) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: Cushman

SA, Huettman F (eds), Spatial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo

- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75(4):580-586
- Garfin G, Franco G, Blanco H, Comrie A, Gonzalez P, Piechota T, Smyth R, Waskom R (2014) Chapter 20: Southwest. In: Melillo JM, Richmond TC, Yohe GW (eds), Climate Change Impacts in the United States: the Third National Climate Assessment. U.S. Global Climate Change Research Program, Washington, D.C.
- Gustafson EJ, Gardner RH (1996) The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77(1):94-107
- Hansen AJ, Piekielek N, Davis C, Haas J, Theobald DM, Gross JE, Monahan WB, Olliff T, Running SW(2013) Exposure of U.S. national parks to land use and climate change 1900–2100. Ecological Applications 24(3):484-502
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470(7335):479-485
- Holderegger R, Kamm U, Gugerli F (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. Landscape Ecology 21(6):797-807
- Keller D, Holderegger R, van Strien M, Bolliger J (2015) How to make landscape genetics beneficial for conservation management? Conservation Genetics 16(3):503-512
- Krausman PR, Sandoval AV, Etchberger RC (1999) Natural history of desert bighorn sheep. In: Valdez R and Krausman PR (eds), Mountain Sheep of North America. University of Arizona Press, Tucson, AZ
- Leslie DM, Douglas CL (1980) Human disturbance at water sources of desert bighorn sheep. Wildlife Society Bulletin 8(4):284-290
- Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution 18(4):189-197
- McNaughton SJ (1990) Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345(6276):613-615
- Nicotra AB, Beever EA, Robertson AL, Hofmann GE, O'Leary J (2015) Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conservation Biology 29(5):1268-1278
- Papouchis CM, Singer FJ, Sloan WB (2001) Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65(3):573-582
- Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Functional Ecology 23(1):57-69
- Pettorelli N, Pelletier F, Hardenberg Av, Festa-Bianchet M, Côté SD (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88(2):381-390

- Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132(5):652-661
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158(1):87-99
- Risenhoover KL, Bailey JA (1985) Foraging ecology of mountain sheep: implications for habitat management. Journal of Wildlife Management 49(3):797-804
- Rubin ES, Boyce WM, Stermer CJ, Torres SG (2002) Bighorn sheep habitat use and selection near an urban environment. Biological Conservation 104(2):251-263
- Ryan SJ, Cross PC, Winnie J, Hay C, Bowers J, Getz WM (2012) The utility of normalized difference vegetation index for predicting African buffalo forage quality. Journal of Wildlife Management 76(7):1499-1508
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1):18-32
- Schloss CA, Nuñez TA, Lawler JJ (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109(22):8606-8611
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316(5828):1181-1184
- Seager R, Ting M, Li C, Naik N, Cook B, Nakamura J, Liu H (2013) Projections of declining surface-water availability for the southwestern United States. Nature Climate Change 3(5):482-486
- Singer FJ, Gudorf MA (1999) Restoration of bighorn sheep metapopulations in and near 15 national parks: conservation of a severely fragmented species. Volume I: planning, problem definition, key findings, and restoration. U.S. Geological Survey and U.S. Department of the Interior, Open File Report 99-102
- Skelly DK, Joseph LN, Possingham HP, Freidenburg LK, Farrugia TJ, Kinnison MT, Hendry AP (2007) Evolutionary responses to climate change. Conservation Biology 21(5):1353-1355
- Turner MG, Gardner RH, O'Neill RV (2001) Landscape Ecology in Theory and Practice: Pattern and Process. Springer Science+Business Media, New York
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414(6859):65-69
- Wasserman TN, Cushman SA, Littell JS, Shirk AJ, Landguth EL (2012) Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. Conservation Genetics 14(2):1-13
- Wehausen JD, Ramey RR (2000) Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis*. Journal of Mammalogy 81(1):145-161

# USING NETWORK THEORY TO PRIORITIZE MANAGEMENT IN A DESERT BIGHORN SHEEP METAPOPULATION

Tyler G. Creech, Clinton W. Epps, Ryan J. Monello, and John D. Wehausen

Landscape Ecology Springer Science+Business Media LLC, 233 Spring Street, New York, NY 10013-1578 Volume 29, Issue 4, pp. 605-619 (2014)

## CHAPTER 1: USING NETWORK THEORY TO PRIORITIZE MANAGEMENT IN A DESERT BIGHORN SHEEP METAPOPULATION

Tyler G. Creech<sup>1</sup>, Clinton W. Epps<sup>1</sup>, Ryan J. Monello<sup>2</sup>, and John D. Wehausen<sup>3</sup>

<sup>1</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

<sup>2</sup> National Park Service, Biological Resource Management Division, Fort Collins, CO, USA

<sup>3</sup> White Mountain Research Center, University of California, Bishop, CA, USA

## ABSTRACT

Connectivity models using empirically-derived landscape resistance maps can predict potential linkages among fragmented animal and plant populations. However, such models have rarely been used to guide systematic decision-making, such as identifying the most important habitat patches and dispersal corridors to protect or restore in order to maximize regional connectivity. Combining resistance models with network theory offers one means of prioritizing management for connectivity, and we applied this approach to a metapopulation of desert bighorn sheep (Ovis canadensis nelsoni) in the Mojave Desert of the southwestern United States. We used a genetic-based landscape resistance model to construct network models of genetic connectivity (potential for gene flow) and demographic connectivity (potential for colonization of empty habitat patches), which may differ because of sex-biased dispersal in bighorn sheep. We identified high-priority habitat patches and corridors and found that the type of connectivity and the network metric used to quantify connectivity had substantial effects on prioritization results, although some features ranked highly across all combinations. Rankings were also sensitive to our empirically-derived estimates of maximum effective dispersal distance, highlighting the importance of this often-ignored parameter. Patch-based analogs of our network metrics predicted both neutral and mitochondrial genetic diversity of 25 populations within the study area. This study demonstrates that network theory can enhance the utility of landscape resistance models as tools for conservation, but it is critical to consider the implications of sex-biased dispersal, the biological relevance of

network metrics, and the uncertainty associated with dispersal range and behavior when using this approach.

#### INTRODUCTION

Connectivity is a beneficial or necessary component of many ecological processes, including gene flow, migration, dispersal from natal ranges, range shifts in response to climate change, and metapopulation dynamics (Crooks and Sanjayan 2006). The past decade has seen rapid progress in the development of connectivity models that use resistance surfaces to explain effects of landscape features on animal movement (Chardon et al. 2003; Chetkiewicz and Boyce 2009; Perez-Espona et al. 2008). Numerous studies using resistance surfaces have demonstrated that effective distance (ED), which combines geographic distance and relative habitat resistance, is a better predictor of realized population connectivity than simple Euclidean distance (Cushman et al. 2006; Epps et al. 2007; McRae and Beier 2007). Resistance-based connectivity models have facilitated the identification of likely routes for dispersal and movement between habitat patches using methods such as least-cost path (LCP) analysis and circuit theory (Adriaensen et al. 2003; McRae et al. 2008). Although resistance models may perform poorly when resistance values are assigned to different habitats solely on expert opinion (Sawyer et al. 2011; Spear et al. 2010), landscape genetic analyses (e.g., Cushman et al. 2006; Epps et al. 2007) or resource selection models (e.g., Chetkiewicz and Boyce 2009; Epps et al. 2013) can be used to develop and optimize models with an empirical basis. Developing such models has become increasingly popular (Zeller et al. 2012) and empirically-derived resistance models have been used to evaluate or map prospective dispersal corridors (Cushman et al. 2010; Wasserman et al. 2012), but they have rarely been used to guide more systematic decision making. For instance, even knowing the likely location and ED of dispersal routes does not allow rigorous evaluation of their relative importance in metapopulations or other fragmented systems. Because conservation resources are always limited, methods for prioritizing actions are a critical component missing from many connectivity analyses.

Combining landscape resistance models with network theory offers a compelling potential solution. Network theory has risen to prominence in landscape ecology as a

framework for quantifying the role that habitat patches and dispersal corridors play in linking fragmented populations (Urban et al. 2009). In this context, a network consists of "nodes" (habitat patches or populations) and "edges" (connections between populations). Information on actual or potential dispersal between patches determines which nodes are connected by edges, and in some cases the strength of the connection. Network theory offers a multitude of metrics to quantify contributions of individual nodes and edges to network connectivity, and thus could help guide decisions about where to manage, maintain, or restore connectivity. However, defining the location and strength of edges is problematic; many analyses connect nodes on the basis of rough approximations such as the maximum dispersal distance for the species according to telemetry data or expert opinion (e.g., Fortuna et al. 2006; Minor and Urban 2007), ignoring variation in the intervening landscape. As described above, landscape resistance models derived from empirical data allow the construction of network models with edge weight determined by ED rather than geographic distance. Less commonly, resistance models have also been used to estimate maximum effective dispersal distance (Epps et al. 2007; Parks et al. 2012), information that can be used to limit network edges in a more meaningful way. The resulting networks could provide a powerful tool for quantifying the relative importance of each patch and corridor to overall connectivity.

The need to prioritize conservation actions in fragmented systems raises another commonly-neglected point: distinguishing among different types of connectivity may be important. The potential for gene flow among populations (hereafter, "genetic connectivity") and the potential for re-colonization of habitat patches after local extinctions (hereafter, "demographic connectivity") are often cited as critical reasons to maintain connectivity among fragmented populations (Crooks and Sanjayan 2006; Mills 2007), but could potentially operate at different scales if species exhibit sex-biased dispersal. Levels of connectivity that allow for adequate gene flow may not allow for adequate re-colonization, and patches or corridors that are most important to genetic connectivity of a metapopulation may not coincide with those most important to demographic connectivity. This is especially relevant for species with highly sex-biased dispersal, where re-colonization potential may be limited by the more philopatric sex but gene flow is facilitated by both sexes.

Here, we combine resistance-based connectivity models and network theory to develop tools for prioritizing management options in a metapopulation of desert bighorn sheep (Ovis canadensis nelsoni) in the Mojave Desert of southern California and Nevada, USA. Bighorn sheep exhibit sex-biased dispersal (Krausman et al. 1999); therefore, we consider genetic and demographic connectivity explicitly and separately. Bighorn sheep populations in this region occupy numerous small mountain ranges separated by broad expanses of relatively flat desert (Fig. 1.1), and their relative isolation and small size makes them vulnerable to loss of genetic diversity through genetic drift and inbreeding (Epps et al. 2005). Population extinctions occurred in nearly 40% of central Mojave populations over a 60-year period during the 20<sup>th</sup> century (Torres et al. 1994), and there is a clear need to maintain connectivity between habitat patches to allow for re-colonization (Epps et al. 2010). Although core habitat where bighorn sheep reside, forage, and breed remains largely intact in the region, surrounding dispersal habitat has been fragmented over the past century by interstate highways, canals, urbanization, mining operations, and other anthropogenic developments (Epps et al. 2005). In the absence of disease, connectivity is expected to positively affect metapopulation persistence and genetic diversity.

This landscape exemplifies the need for tools to prioritize management actions in fragmented systems. Current and proposed utility-scale renewable energy development could further compromise connectivity if energy facilities such as wind farms or solar arrays are sited in or near bighorn sheep habitat or along dispersal corridors (Lovich and Ennen 2011). Possible management actions to protect connectivity in this system include: 1) establishing additional protections for occupied habitat patches; 2) establishing additional protections for occupied habitat patches; 2) establishing additional protections for intact dispersal corridors; 3) reintroducing bighorn sheep populations in suitable habitat patches that are currently unoccupied; and 4) removing existing barriers to dispersal (e.g., installing wildlife crossing structures). We use genetic-based landscape resistance models from the Mojave bighorn sheep metapopulation to construct network models with three objectives: 1) to establish priorities for maximizing desert bighorn connectivity in the region; 2) to determine how the prioritization process is influenced by the type of connectivity (genetic versus demographic); and 3) to evaluate the impact of model error and assumptions on prioritization results.

#### **METHODS**

Our analysis followed three general steps. First, we used a least-cost path resistance model optimized from genetic data (Epps et al. 2007) to estimate connectivity among habitat patches in the Mojave Desert. Second, we combined these connectivity estimates with genetic estimates of dispersal thresholds to construct network models describing genetic or demographic connectivity. Third, we used network metrics to rank the importance of each patch and corridor with respect to network connectivity, and explored sensitivity of rankings to connectivity type, network metric, and modeling error.

#### **Study area**

We defined our study area to match the spatial extent of the analyses in Epps et al. (2007), including 37 habitat patches currently occupied by bighorn sheep populations (Fig. 1.1). Because bighorn sheep use steep terrain almost exclusively, patch boundaries were delineated on the basis of slope (>10%) and effective distance to perennial water sources (see Appendix 2 of Epps et al. 2007); in some cases, boundaries were modified using expert opinion to include additional area known to be used by bighorn sheep. Each population was associated with a single patch and represented by a single network node because bighorn habitat is discretely distributed on the landscape, and previous genetic analyses supported these patch-based population. (Epps et al. 2005, 2007); thus, we hereafter use the terms "patch," "population," and "node" interchangeably. We also identified 13 "restorable patches" in the study area that currently do not support a bighorn sheep population but did in the past (Epps et al. 2004; Wehausen 1999) and are within dispersal range of an occupied patch.

Connectivity with patches beyond the boundary of our study area is likely, which creates the potential for bias in the network analysis: patches near the boundary may appear relatively unimportant even if they provide important connections to patches outside the boundary. To minimize this bias, we included occupied "buffer" patches adjacent to our study area (n = 8), but did not evaluate potential management actions among those buffer patches.

#### **Genetic-based connectivity models**

We inferred connectivity using a landscape resistance model developed by Epps et al. (2007) that used gene flow estimates among populations of desert bighorn sheep (392)

individuals; 26 populations; 14 microsatellite loci) to test and optimize least-cost path connectivity models incorporating distance and topography and estimated dispersal thresholds in terms of ED from the best model. We believe least-cost path models better approximate ED for bighorn sheep in this system than alternative methods that incorporate less efficient dispersal routes (e.g., circuit theory, least-cost corridor) because habitat patches are discrete mountain ranges separated by desert flats, allowing bighorn sheep to see for long distances to other habitat patches within the scale of individual movements and to visually navigate between patches. Epps et al. (2007) used partial Mantel tests to compare 18 topography-based resistance models representing all combinations of three percent-slope cutoffs between high- and low-resistance slope categories, and six ratios of high:low resistance values. The strongest correlation between ED and gene flow occurred when areas of >15% slope were assigned 1/10<sup>th</sup> the dispersal cost of areas of <15% slope. The estimated maximum effective dispersal distance (ED<sub>MAX</sub>) was 16.4 resistance units (referred to as "km-cost-units" in Epps et al. 2007; equivalent to 16.4 km of <15%-slope terrain, or 164 km of >15%-slope terrain).

Bighorn sheep exhibit sex-biased dispersal, with males moving between patches more frequently and over greater distances than females (Krausman et al. 1999). Because the Epps et al. (2007) model was developed from bi-parentally inherited genetic markers, it is suitable for describing gene flow but likely overestimates the potential for recolonization or rescue, which are limited by female dispersal. Thus, a female-specific estimate of  $ED_{MAX}$  was needed to characterize demographic connectivity. We estimated female  $ED_{MAX}$  using two sources of data: 1) observations of radio-collared females moving between patches, and 2) sharing of female mitochondrial haplotypes between patches, which indicate past female dispersal events given that mitochondrial DNA is maternally inherited (explained fully in Appendix B). The frequency distribution of ED for female dispersal events (Fig. B.1) suggested female dispersal declined with ED at a rate similar to that observed by Epps et al. (2007) for male-limited gene flow, but with a smaller ED<sub>MAX</sub>. We modified the equation from Epps et al. (2007) predicting gene flow as a function of ED to account for this reduced dispersal range, and explored sensitivity to errors of up to 30% in the estimation of female ED<sub>MAX</sub> (Appendix C). We calculated the ED of the least-cost paths between all pairs of habitat patches in the study area (including buffer patches and patches for which genetic data were unavailable) using the slope-based resistance model described above. Anthropogenic features acting as complete or nearly complete barriers to bighorn sheep dispersal based on anecdotal evidence (Bleich et al. 1996) or genetic analysis (Epps et al. 2005), including fenced interstate highways, urban areas, and aqueducts, were incorporated into resistance surfaces by assigning barrier cells a million times higher resistance than nonbarrier cells; this ensured that the least-cost path between any pair of patches separated by a barrier had ED > ED<sub>MAX</sub>. Least-cost paths were calculated in ArcGIS 10.0 (ESRI, Redlands, CA, USA). We then used ED values to predict expected gene flow (*Nm*; see Equation 2 in Epps et al. 2007) between each pair of patches. While the interpretation of *F*<sub>ST</sub>-based estimates of *Nm* has been questioned (Holsinger and Weir 2009; Whitlock and McCauley 1999), we used *Nm* merely as a measure of relative differences in gene flow among pairs of habitat patches.

### Network models

We generated two network models to explore genetic and demographic connectivity of the Mojave bighorn sheep metapopulation:

- Genetic network: This network modeled the potential for gene flow among patches, which should be limited by male dispersal range. We included network edges representing dispersal corridors between all pairs of patches separated by ED < 16.4 resistance units (and hereafter use the terms "edge" and "corridor" interchangeably). We then assigned these corridors weights equal to their predicted *Nm* values (Appendix B); thus, within the estimated maximum male dispersal range, the strength of dispersal varied with effective distance as predicted by the genetic-based resistance model. We assumed gene flow between connected patches was symmetrical; the validity of this assumption is discussed later.
- Demographic network: This network modeled the potential for rescue or recolonization of a patch from neighboring patches, which should be limited by female dispersal range. Accordingly, we included corridors between all pairs of patches separated by ED < 10 resistance units, our estimate of maximum female dispersal distance (Appendix B). Similar to the genetic network, corridors were weighted by

the female-specific *Nm*-ED equation (Appendix B), and we assumed symmetrical dispersal. Thus, the demographic network was a sparser version of the genetic network, containing all of the same patches but only a subset of the corridors due to the more restricted movement of females.

**Evaluating contribution of individual patches and corridors to connectivity** We used an iterative approach to evaluate the importance of patches and corridors to network connectivity. First, we identified subsets of network features that could be targeted for each of four possible management actions. The "patch protection" (PP) subset included all patches in the current network, and the "patch restoration" (PR) subset included all restorable patches within ED<sub>MAX</sub> of a patch in the study area. The "corridor protection" (CP) subset included all corridors in the current network, and the "corridor restoration" (CR) subset included all potentially restorable corridors that are currently interrupted by an anthropogenic barrier but would otherwise connect two patches separated by <ED<sub>MAX</sub>. These subsets differed between the genetic and demographic networks because these networks included different numbers of restorable patches, corridors, and restorable corridors due to differences in ED<sub>MAX</sub>.

For PP and CP, we deleted one patch or corridor at a time and then re-calculated network metrics (discussed below) to determine the effect of that specific feature on network connectivity. Patches and corridors whose removal resulted in larger decreases in network connectivity metrics were inferred to be more important contributors to genetic or demographic connectivity, and higher priority for protection. Because redundant corridors were excluded from the network (Appendix B), our method assumed that the loss of a patch compromised all corridors passing through that patch. For PR and CR, we added one patch or corridor at a time and re-calculated network metrics; patches and corridors whose addition resulted in larger increases in network connectivity metrics were inferred to be higher priority for restoration.

Contributions of individual nodes and edges to network connectivity can be assessed using a wide variety of network metrics, but choosing a biologically appropriate metric to describe a particular aspect of connectivity is challenging (Moilanen 2011; Pascual-Hortal and Saura 2006). Global metrics that describe whole network-level properties can be used to describe the impact of specific network features on connectivity
by comparing these metrics for networks with and without a particular node or edge. However, many global metrics are not calculable or not meaningful when applied to fragmented networks consisting of multiple disconnected subgroups of patches ("components"), which are common among anthropogenically-fragmented systems such as ours. We used two metrics that describe network-level connectivity but are unaffected by multiple components (see additional details in Appendix D):

- 1. *Mean weighted closeness (MWC)*. Closeness is a measure of how near a patch is to all other network patches along shortest paths and can be calculated in weighted networks using Dijkstra's (1959) algorithm, which accounts for the possibility that paths containing many steps of large weight may be more efficient than paths containing few steps of small weight. We used a formulation of weighted closeness for networks with disconnected components (Opsahl et al. 2010) and calculated the mean of this metric across all patches. MWC reflects the long-term potential for transfer of genes or individuals across the network because it considers all connections, including those between very distant patches that would require numerous dispersal steps. Network changes (e.g., patch or corridor additions) that increase MWC can be interpreted as increasing the efficiency of transfer for genes or individuals within the network over multiple generations.
- Effectively connected pairs (ECP). We defined this metric as the number of pairs of patches connected by a total effective distance less than ED<sub>MAX</sub> (i.e., <16.4 resistance units in the genetic network and <10 resistance units in the demographic network). This included pairs that are connected by a single corridor or a multi-corridor path with combined effective distance < ED<sub>MAX</sub>. ECP describes the short-term potential for genetic or demographic connectivity among populations.

For each management action, we calculated the proportional change (hereafter,  $\Delta$  value) in network metrics when each feature was removed from the network (for PP and CP) or added to the network (for PR and CR). Larger  $\Delta$  values indicate features with a larger positive impact on connectivity.

To determine how the type of connectivity affected prioritization results, we calculated Spearman's rank correlation coefficient between genetic network  $\Delta$  values and demographic network  $\Delta$  values for each metric (ECP or MWC) and type of management

action (PP, CP, PR, or CR). We also calculated the Spearman correlation between ECPand MWC-based  $\Delta$  values within each network to determine how metric choice affected prioritization. In cases where between-network comparisons involved different numbers of patches or corridors, we calculated correlations using  $\Delta$  values for those features common to both networks. Lastly, we identified "high-priority" patches or corridors for each management action as those ranking among the top 5 in at least two of the four combinations of connectivity type and network metric.

#### Sensitivity analysis

We evaluated sensitivity to changes in male and female ED<sub>MAX</sub> (which define corridor presence/absence) by increasing or decreasing ED<sub>MAX</sub> in 5-percent increments up to 30% (male ED<sub>MAX</sub>: 11.5 – 21.3, female ED<sub>MAX</sub>: 7.0 - 13.0 resistance units). We then reanalyzed the data to produce new sets of  $\Delta$  values at each error level, and we calculated the Spearman correlation between  $\Delta$  values from original ED<sub>MAX</sub> estimates and  $\Delta$  values at each error level. We also examined how the set of features identified as potential targets for each management action changed as a function of ED<sub>MAX</sub> (see Appendix C for further details).

#### **Testing ecological relevance of network metrics**

Connectivity measures, especially network metrics, have been criticized for having questionable relevance to ecological processes such as gene flow or colonization (Moilanen 2011; Pascual-Hortal and Saura 2006). We tested the relevance of our network-level metrics (ECP and MWC) by generating patch-level analogs and determining whether they predicted nuclear and mitochondrial genetic diversity of patches in the genetic and demographic networks, respectively. If the structures of our networks adequately represent gene flow and colonization, and ECP and MWC adequately capture these processes at the metapopulation level, then we would expect that patch-level analogs of ECP and MWC should be correlated with: 1) allelic richness (*A*) and expected heterozygosity ( $H_e$ ) of patches in the genetic network, which should be influenced most by male-mediated gene flow, and 2) mitochondrial haplotype richness (*HR*) of patches in the demographic network, which should reflect female movements between populations because mitochondrial haplotypes are maternally inherited (see Appendix E).

#### RESULTS

As expected, the genetic network exhibited much greater connectivity than the demographic network (Fig. 1.2). The genetic network contained nearly twice as many corridors (gen: 66, dem: 38) and effectively connected pairs (gen: 122, dem: 65), and fewer than half as many components as the demographic network (gen: 5, dem: 13). MWC was nearly twice as high in the genetic network than the demographic network (gen: 11.57, dem: 5.83). We report additional network properties in Appendix F to facilitate comparison with other ecological networks.

We identified 21 restorable corridors and 13 restorable patches in the genetic network, and 15 restorable corridors and 11 restorable patches in the demographic network. Prioritization of patches and corridors varied between genetic and demographic networks, and also between metrics (Tables 1.1, G.1-G.4; Figs. 1.2, G.1-G.4). Correlations between  $\Delta$  values from the genetic and demographic networks ranged from 0.62 to 0.95 depending on which management action and metric was considered. Within a network type, correlations between ECP- and MWC-based  $\Delta$  values ranged from 0.35 to 0.95; for all management actions except corridor restoration, these between-metric correlations were higher in the demographic network than the genetic network. Although some of these correlation values were quite low, agreement among the top ranking features was generally much better than among the entire set of features (Tables 1.2, G.1-G.4). We identified at least four patches or corridors for each management action that met our criteria for high-priority features (Table 1.2).

Sensitivity analysis showed that  $\Delta$  values were generally quite robust to errors in ED<sub>MAX</sub>, although this varied across combinations of management action, connectivity type (genetic vs. demographic), and network metric (Fig. C.1). The correlation of original  $\Delta$  values with new  $\Delta$  values remained above 0.75 within the range of ED<sub>MAX</sub> values tested (±30%), with the exception of MWC-based results in the genetic network, which changed considerably when ED<sub>MAX</sub> was reduced by more than 20%. However, changing ED<sub>MAX</sub> led to changes in the subsets of nodes and edges identified as potential targets for each management action (Figs. C.2, C.3). For instance, decreasing female ED<sub>MAX</sub> by 30% meant that only 65% of the restorable corridors identified in our analysis would still meet the criteria for a restorable corridor.

Patch-based analogs of our network metrics calculated for the genetic network predicted both A and  $H_e$  ( $R^2 = 0.19 - 0.34$ ; P = 0.002 - 0.029), and those calculated for the demographic network predicted HR ( $R^2 = 0.53 - 0.56$ ; P < 0.0001), for 25 populations within our study system (Appendix E, Table E.1). Our patch-level analogs of ECP and MWC explained considerably more variation in all three genetic diversity indices than common centrality metrics (Table E.1), suggesting that ECP and MWC have greater ecological relevance as measures of connectivity, although much of the variation in genetic diversity remained unexplained.

#### DISCUSSION

Recognition of the need to prioritize management (including restoration) of habitat patches and corridors at the landscape scale is increasing, as evidenced by recent publications addressing this issue using resistance- or network-based approaches (Albert et al. 2013; McRae et al. 2012; Theobald et al. 2012). Yet, very rarely have these two approaches been combined to achieve greater insight into the effects of potential management actions, as demonstrated by our analysis. One exception is Lookingbill et al. (2010), who used network theory to evaluate the relative importance of existing dispersal corridors and habitat patches for the Delarma fox squirrel (*Sciurus niger cinereus*); that analysis used an individual-based simulation model of dispersal across an expert opinionbased resistance surface to estimate connectivity among patches and construct a binary network. We further refined this methodology by: 1) utilizing an optimized, empiricallyderived resistance model, 2) constructing weighted networks that incorporate differences in effective distances among corridors (i.e., edge weights); 3) considering patch and corridor restorations in addition to losses; and 4) evaluating multiple types of connectivity. This combined approach provides a useful framework for distinguishing among different processes related to connectivity, as well as an objective means of balancing those biological elements in our decision-making.

We observed large structural differences between networks based on genetic connectivity and those based on demographic connectivity (Fig. 1.2), with much higher levels of both short-term (ECP) and long-term (MWC) connectivity in the genetic network. Therefore, managing to maintain only genetic connectivity among bighorn sheep populations would not necessarily maintain natural re-colonization; likewise, important connections for gene flow might be missed if only colonization potential was considered. This pattern is probably common among species that exhibit strongly sexbiased dispersal. For such species, researchers and managers must give greater recognition to the type of connectivity that they are trying to model, preserve, or restore.

Considering different types of connectivity resulted in markedly different prioritization results for some management actions (Table 1.1, G.1-G.4). However, there was generally strong agreement among the highest ranking features in each network according to one or both of our metrics. For each management action, we found at least four high-priority features and at least two features that ranked in the top five across all four combinations of connectivity type and network metric (Table 1.2), suggesting that conservation actions could target patches or corridors that are highly important to both genetic and demographic connectivity and to both short- and long-term connectivity. Consistent with previous network-based connectivity analyses (Jordán et al. 2003; Laita et al. 2011), prioritization also depended on the choice of network metric (Table 1.1), reinforcing the need to select biologically relevant network metrics. We chose our two metrics to represent local and long-distance transfer of genes or individuals in a bighorn sheep metapopulation, but recognize that these metrics cannot capture all aspects of those processes.

Our sensitivity analysis suggested that values of connectivity metrics were relatively robust to errors in estimating  $ED_{MAX}$  (Appendix C). However, such errors were quite influential in determining which features should be candidates for a particular management action. For instance, the Avawatz-S. Soda (AVA-SSO) corridor was the highest ranking restorable corridor by MWC in the demographic network (Table G.4), but if female  $ED_{MAX}$  was decreased by only 10%, the AVA-SSO corridor's ED would be too large for it to be considered a restorable corridor. Thus, even small errors in estimating dispersal thresholds or dispersal functions, or estimates that ignore landscape resistance, could affect conclusions about the relative importance of patches and corridors to network connectivity. Estimating dispersal functions and thresholds remains a challenging research need and a major limitation to many connectivity analyses (Parks et al. 2012).

#### **Analytical limitations**

Our networks were constructed using the topography-based Epps et al. (2007) landscape resistance model, and the parameterization of that landscape resistance model could affect our conclusions about the relative importance of network features. Incorporating other environmental variables in the resistance model could influence network rankings, although Epps et al. (2007) observed a strong relationship between genetic differentiation and effective distance using the topographic resistance model. Additionally, resistance models were tested using partial Mantel tests, which have been demonstrated to have inflated risk of type I error when applied to spatially autocorrelated data (Graves et al. 2013; Guillot and Rousset 2013); however, the best model was identified on the basis on Mantel r correlation, not statistical significance, and had a very small p-value (<0.0001, unpublished data).

We assumed that dispersal between patches is symmetrical, but this may be an oversimplification. Because habitat quality varies among patches (Epps et al. 2004, 2006), source-sink dynamics could influence dispersal. Network theory can easily accommodate asymmetrical connectivity, but genetic methods for estimating directional dispersal are less well established.

Our prioritization assumed that only a single patch or corridor was added or removed to the existing network. Consequently, if multiple actions were taken simultaneously, it would be incorrect to conclude that the greatest benefit to connectivity would result from pursuing actions in order of their  $\Delta$  values. For instance, if the two restorable corridors with the highest  $\Delta$  values in the genetic network were restored (the Granite-Marble [GRA-MAR] and N. Bristol-S. Bristol [NBR-SBR] corridors; Table G.4; Fig. G.1), they would play nearly identical roles by linking the two largest network components across Interstate Highway 40. Restoring the GRA-MAR corridor and a corridor across a different barrier (e.g., the Eagle-Orocopia [EMO-ORO] corridor across Interstate Highway 10) would be more useful. We strongly recommend grouping restorable corridors by the barrier feature with which they are associated, then using our results to prioritize within each group rather than on the basis of overall ranks.

Additional factors beyond the contribution of patches and corridors to metapopulation connectivity will need to be considered when prioritizing management.

Monetary costs, conflicts with other land uses, effects on other species, effects on disease spread, and public support are all likely to vary by management action and location. Information on habitat quality (e.g., Epps et al. 2004) may also allow more efficient use of management resources than relying solely on network connectivity rankings. Consideration of these factors is beyond the scope of this analysis; here, we have sought only to provide input on the biological connectivity aspect of the overall prioritization process.

#### **Recommended actions in the Mojave Desert region**

Should conservation resources be allocated preferentially to patch- or corridor-focused actions? Using  $\Delta$  values to compare patch protection versus corridor protection is not informative because our analysis assumed that the loss of a patch also compromised all associated corridors (a necessary assumption because network methods require that every edge connects two nodes). However, comparisons between patch restoration and corridor restoration effectiveness on the basis of  $\Delta$  values are warranted. Corridor restorations had a much stronger effect on long-term connectivity (as measured by MWC) than patch restorations in both the genetic and demographic network: 18 of 21 restorable corridors in the genetic network and 9 of 15 in the demographic network would increase MWC more than the top-ranked restorable patch (Tables G.3, G.4). If increasing short-term connectivity is the goal, however, then patch restorations could be nearly as effective: only 4 restorable corridors in the genetic network and 2 in the demographic network would increase ECP more than the top-ranked restorable patch (Tables G.3, G.4). There may be fewer new opportunities for patch protection than corridor protection in our study area because the current system of land protection (e.g., Wilderness designation) focuses more on core bighorn sheep habitats (i.e., mountain ranges) than infrequently used dispersal habitat. Yet, patch protection and restoration through natural colonization or population reintroductions are still vital to maintain metapopulation viability. Restoring corridors to unoccupied patches could be warranted when a patch contains favorable bighorn sheep habitat but has experienced a population extinction due to stochastic or temporary factors (e.g., local drought or disease outbreak) and has not had opportunity to be naturally recolonized; in such cases, restoring connectivity could make population reintroduction efforts unnecessary.

Our network approach is also amenable to evaluating conservation actions targeting multiple patches or corridors. For example, we used our models to quantify the effects of four plausible multi-feature restoration scenarios: 1) re-occupation of N. Soda (NSO) patch and restoration of the NSO-SSO, GRA-MAR, and EMO-ORO corridors to mitigate barrier effects of three interstate highways; 2) re-occupation of four northern patches (Fort Irwin Granite [FIG], Owlshead [OWL], Quail [QUA], and Slate [SLA]) that are currently unoccupied but have low predicted extinction probabilities (Epps et al. 2004); 3) re-occupation of the Sacramento (SAC) and Piute (PIU) patches to provide stepping stones between eastern and central patches in the metapopulation; and 4) all of the above actions. Scenario 1 is the most efficient of the individual scenarios for increasing MWC because it links together the four largest components in the network (Table 1.3). Scenario 1 is also most efficient for increasing ECP in the genetic network, but slightly less efficient than Scenario 2 in the demographic network. Dramatic increases in metapopulation connectivity are possible by combining patch and corridor restorations: under Scenario 4, ECP and MWC would more than double in the genetic and demographic networks.

We suggest several actions to efficiently maximize genetic diversity and metapopulation persistence in the Mojave region. First, restore at least one connection across each of the three interstate highways that currently fragment the metapopulation, which will vastly improve the potential for long-distance gene flow in this system and restore important demographic links (Epps et al. 2005). Second, evaluate whether existing infrastructure such as highway bridges over washes can be modified to encourage use by bighorn sheep; for instance, by removing highway fencing around bridged washes and strategically locating artificial water sources to lure sheep to the area, it may be possible to facilitate bighorn sheep crossings beneath highways in some locations. Third, maximize patch occupancy by protecting or improving habitat, protecting routes for natural re-colonization (even to currently unoccupied patches), or reintroducing populations where natural re-colonization is unlikely. Finally, we note that our rankings could be used to address situations where connectivity is potentially problematic. For instance, our rankings may indicate which populations or connections could have the greatest impact on disease spread, such as in response to a recent outbreak of respiratory disease within the study area (California Dept. of Fish and Wildlife, unpublished data).

#### Applying the network approach in conservation

Combining landscape resistance models with network analysis offers a means of evaluating conservation scenarios across complex systems. Other studies of genetic connectivity have used genetic data alone (e.g., pairwise genetic distances) to construct network models (Dyer and Nason 2004; Garroway et al. 2008; Rozenfeld et al. 2008). The advantage of this approach is that it quantifies genetic connectivity between populations more directly than the resistance-based approach we used. However, it can only be applied to extant populations for which genetic data are available, and assumes that genetic distance reflects the current landscape configuration. In contrast, our resistance-based approach can be used to predict connectivity between any set of habitat patches and to evaluate effects of barrier mitigation or population reintroduction. However, we reiterate that evaluating how dispersal varies with effective distance is an important component when combining resistance models with network analysis, and better methods of estimating such relationships are needed.

Evaluating the relative importance of habitat patches and dispersal corridors by iterative removal from and addition to network models is particularly useful when the spatial footprint of potential threats to habitat or connectivity is unclear. For instance, the transitory nature of renewable energy development plans in the Mojave Desert makes it difficult to anticipate the specific locations and extents of energy facilities with any certainty. Incorporating anticipated landscape changes directly into resistance surfaces and re-analyzing network structure might be preferable, but it may be too late for meaningful conservation action by the time that final development plans are available. Instead, the iterative prioritization method can be used to evaluate landscape changes in accordance with the importance of the patches and edges likely to be affected due to their proximity.

Conservation applications of network theory have been criticized for overemphasizing the relevance of landscape connectivity (Moilanen 2011), which is only one of several factors contributing to regional persistence – the ultimate goal of most conservation programs. More complex metapopulation models allow for estimation of

persistence probabilities and have also been used to prioritize habitat patches and dispersal corridors (Hoyle and James 2005; Moilanen et al. 1998); yet the data requirements for such models are prohibitive even in many well-studied systems, limiting their application to real-world conservation issues. For instance, the well-known incidence function model (Hanski 1994) requires estimates of patch-specific colonization and extinction rates that are typically obtained through multi-year occupancy surveys of all possible habitat patches. Obtaining these empirical estimates for species with slow population turnover rates, such as desert bighorn sheep, is simply not feasible within a short enough time frame to inform management decisions. For example, Epps et al. (2010) reported only 4 known desert bighorn colonization events in a 20 year period in the Mojave Desert. On the other hand, there is abundant evidence that: 1) re-colonization is critical for persistence of any fragmented system where population extinction is common (Levins 1969) such as the Mojave bighorn system (Epps et al. 2004); 2) genetic diversity affects fitness and ultimately population persistence, particularly for species with small effective population sizes (Frankham 2005; Reed and Frankham 2003); and 3) gene flow between populations is a primary driver of genetic diversity in this system (Epps et al. 2006) and other systems of small, partly-fragmented populations. Thus, clear biological reasons exist for attempting to maximize genetic and demographic connectivity through conservation actions, even when estimates of their effect on regional persistence are not possible.

#### ACKNOWLEDGMENTS

Funding for this research was provided by the National Park Service Climate Change Response Program and Oregon State University. We thank David Theobald and two anonymous reviewers for comments that greatly improved the manuscript.

#### LITERATURE CITED

- Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64(4):233-247
- Albert EM, Fortuna MA, Godoy JA, Bascompte J (2013) Assessing the robustness of networks of spatial genetic variation. Ecology Letters 16:86-93

- Bleich VC, Wehausen JD, Ramey II RR, Rechel JL (1996) Metapopulation theory and mountain sheep: implications for conservation. In: McCullough DR (ed), Metapopulations and Wildlife Conservation. Island Press, Covelo, CA
- Chardon J, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the speckled wood butterfly (*Pararge aegeria* L.). Landscape Ecology 18(6):561-573
- Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46(5):1036-1047
- Crooks KR, Sanjayan MA (2006) Connectivity Conservation. Cambridge University Press, Cambridge
- Cushman SA, Chase M, Griffin C (2010) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: Cushman SA, Huettman F (eds), Spatial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo
- Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. The American Naturalist 168(4):486-499
- Dijkstra EW (1959) A note on two problems in connexion with graphs. Numerische Mathematik 1(1):269-271
- Dyer RJ, Nason JD (2004) Population Graphs: the graph theoretic shape of genetic structure. Molecular Ecology 13(7):1713-1727
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, L. Rechel J (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, McCullough DR (2006) Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15(14):4295-4302
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wasser SK, Keim JL, Mutayoba BM, Brashares JS (2013) Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. Molecular Ecology
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Epps CW, Wehausen JD, Palsbøll PJ, McCullough DR (2010) Using genetic tools to track desert bighorn sheep colonizations. Journal of Wildlife Management 74(3):522-531
- Fortuna MA, Gómez-Rodríguez C, Bascompte J (2006) Spatial network structure and amphibian persistence in stochastic environments. Proceedings of the Royal Society B: Biological Sciences 273(1592):1429-1434

Frankham R (2005) Genetics and extinction. Biological Conservation 126(2):131-140

Garroway CJ, Bowman J, Carr D, Wilson PJ (2008) Applications of graph theory to landscape genetics. Evolutionary Applications 1(4):620-630

- Graves TA, Beier P, Royle JA (2013) Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Molecular Ecology 22(15):3888-3903
- Guillot G, Rousset F (2013) Dismantling the Mantel tests. Methods in Ecology and Evolution 4(4):336-344
- Hanski I (1994) A practical model of metapopulation dynamics. Journal of Animal Ecology 63(1):151-162
- Holsinger KE, Weir BS (2009) Genetics in geographically structured populations: defining, estimating and interpreting F<sub>ST</sub>. Nature Reviews Genetics 10(9):639-650
- Hoyle M, James M (2005) Global warming, human population pressure, and viability of the world's smallest butterfly. Conservation Biology 19(4):1113-1124
- Jordán F, Báldi A, Orci KM, Rácz I, Varga Z (2003) Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a *Pholidoptera transsylvanica* (Orthoptera) metapopulation. Landscape Ecology 18(1):83-92
- Krausman PR, Sandoval AV, Etchberger RC (1999) Natural history of desert bighorn sheep. In: Valdez R and Krausman PR (eds), Mountain Sheep of North America. University of Arizona Press, Tucson, AZ
- Laita A, Kotiaho J, Mönkkönen M (2011) Graph-theoretic connectivity measures: what do they tell us about connectivity? Landscape Ecology 26(7):951-967
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the ESA 15(3):237-240
- Lookingbill TR, Gardner RH, Ferrari JR, Keller CE (2010) Combining a dispersal model with network theory to assess habitat connectivity. Ecological Applications 20(2):427-441
- Lovich JE, Ennen JR (2011) Wildlife conservation and solar energy development in the desert southwest, United States. BioScience 61(12):982-992
- McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104(50):19885-19890
- McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89(10):2712-2724
- McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS ONE 7(12):e52604
- Mills L (2007) Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing, Malden, MA
- Minor ES, Urban DL (2007) Graph theory as a proxy for spatially explicit population models in conservation planning. Ecological Applications 17(6):1771-1782
- Moilanen A (2011) On the limitations of graph-theoretic connectivity in spatial ecology and conservation. Journal of Applied Ecology 48(6):1543-1547
- Moilanen A, Smith Andrew T, Hanski I (1998) Long-term dynamics in a metapopulation of the American pika. The American Naturalist 152(4):530-542
- Opsahl T, Agneessens F, Skvoretz J (2010) Node centrality in weighted networks: generalizing degree and shortest paths. Social Networks 32(3):245-251

- Parks SA, McKelvey KS, Schwartz MK (2012) Effects of weighting schemes on the identification of wildlife corridors generated with least-cost methods. Conservation Biology:145-154
- Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21(7):959-967
- Perez-Espona S, Perez-Barberia FJ, McLeod JE, Jiggins CD, Gordon IJ, Pemberton JM (2008) Landscape features affect gene flow of Scottish Highland red deer (*Cervus elaphus*). Molecular Ecology 17(4):981-996
- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17(1):230-237
- Rozenfeld AF, Arnaud-Haond S, Hernández-García E, Eguíluz VM, Serrão EA, Duarte CM (2008) Network analysis identifies weak and strong links in a metapopulation system. Proceedings of the National Academy of Sciences 105(48):18824-18829
- Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology 48(3):668-678
- Spear SF, Balkenhol N, Fortin M-J, McRae BH, Scribner KIM (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19(17):3576-3591
- Theobald DM, Reed SE, Fields K, Soulé M (2012) Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. Conservation Letters 5(2):123-133
- Torres SG, Bleich VC, Wehausen JD (1994) Status of bighorn sheep in California, 1993. Desert Bighorn Council Transactions 38:17-28
- Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. Ecology Letters 12(3):260-273
- Wasserman TN, Cushman SA, Littell JS, Shirk AJ, Landguth EL (2012) Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. Conservation Genetics:1-13
- Wehausen JD (1999) Rapid extinction of mountain sheep populations revisited. Conservation Biology 13(2):378-384
- Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration:  $F_{ST} \neq 1/(4Nm+1)$ . Heredity 82(2):117-125
- Zeller K, McGarigal K, Whiteley A (2012) Estimating landscape resistance to movement: a review. Landscape Ecology 27(6):777-797

# **TABLES AND FIGURES**

Table 1.1. Correlation of prioritization results between networks and between metrics for each management action. "Set 1" and "Set 2" describe the two sets of  $\Delta$  values being compared. For instance, the first row of the table shows the correlation between ECP-based  $\Delta$  values for patch protection in the genetic network ("Set 1") and ECP-based  $\Delta$  values for patch protection in the demographic network ("Set 2").

	Set 1				Set 2			
	Network <sup>a</sup>	Mgmt. action <sup>b</sup>	Metric <sup>c</sup>	Network	twork Mgmt. Me Action Me		correlation coefficient	
	G	PP	ECP	D	PP	ECP	0.88	
Between-network correlations	G	PP	MWC	D	PP	MWC	0.62	
	G	PR	ECP	D	PR	ECP	0.88	
	G	PR	MWC	D	PR	MWC	0.95	
	G	CP	ECP	D	CP	ECP	0.80	
	G	CP	MWC	D	CP	MWC	0.78	
	G	CR	ECP	D	CR	ECP	0.82	
	G	CR	MWC	D	CR	MWC	0.85	
	G	PP	ECP	G	PP	MWC	0.74	
stween-metric correlations	D	PP	ECP	D	PP	MWC	0.95	
	G	PR	ECP	G	PR	MWC	0.85	
	D	PR	ECP	D	PR	MWC	0.92	
	G	CP	ECP	G	CP	MWC	0.77	
	D	CP	ECP	D	CP	MWC	0.80	
Bé	G	CR	ECP	G	CR	MWC	0.46	
	D	CR	ECP	D	CR	MWC	0.35	

<sup>a</sup> G = genetic network, D = demographic network

<sup>b</sup> PP = patch protection, PR = patch restoration, CP = corridor protection, CR = corridor restoration

<sup>c</sup> ECP = effectively connected pairs, MWC = mean weighted closeness

		Genetic network			Demographic network			
Mgmt. action	Patch or corridor <sup>a</sup>	ECP	MWC	$n^b$	ECP	MWC	n	
	PRO	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$	37	
Datah	PCC	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$		
Patch	GRA	$\checkmark$		37	$\checkmark$	$\checkmark$		
protection	NBR	$\checkmark$			$\checkmark$	$\checkmark$		
	CAD	$\checkmark$			$\checkmark$	$\checkmark$		
	PIN	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$	11	
D ( 1	OWL	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$		
Patch	FIG	$\checkmark$	$\checkmark$	13	$\checkmark$	$\checkmark$		
restoration	SLA	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$		
	QUA		$\checkmark$		$\checkmark$	$\checkmark$		
	GRA-PRO	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$	27	
<b>a</b>	GRA-NBR	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$		
Corridor	CAD-NBR	$\checkmark$		47	$\checkmark$	$\checkmark$		
protection	CSS-KME	$\checkmark$			$\checkmark$	$\checkmark$		
	CAD-SSO	$\checkmark$			$\checkmark$	$\checkmark$		
	GRA-MAR	$\checkmark$	$\checkmark$		$\checkmark$	$\checkmark$		
Corridor	NBR-SBR	$\checkmark$	$\checkmark$	01	$\checkmark$	$\checkmark$	15	
restoration	EMO-ORO	$\checkmark$		21	$\checkmark$	$\checkmark$		
	CLI-PRO		$\checkmark$			$\checkmark$		

Table 1.2. High priority patches and corridors for protection or restoration in the genetic and demographic networks. High priority features are defined as those ranking among the top 5 (represented with a  $\checkmark$  in the table) in at least two of the four combinations of connectivity type (genetic, demographic) and network metric (ECP, MWC).

<sup>a</sup> See Table A.1 for 3-letter patch abbreviations and full patch names

 $^{b}$  n = total number of features associated with a particular management action in the genetic or demographic network

	Genetic network		Demo netv	graphic work
	ECP	MWC	ECP	MWC
Scenario 1: mitigate interstate highways	0.57	0.93	0.46	0.65
Scenario 2: re-occupy northern Mojave patches	0.35	0.18	0.48	0.33
Scenario 3: re-occupy stepping stone patches	0.07	0.06	0.05	0.02
Scenario 4: all actions in scenarios 1-3	1.16	1.27	1.02	1.07

Table 1.3. Effects of four multi-part conservation scenarios on connectivity of genetic and demographic networks, as measured by  $\Delta$  values associated with each scenario for both network types and metrics.



Figure 1.1. Desert bighorn sheep habitat patches in the Mojave Desert region. Gray polygons are occupied patches, white polygons are unoccupied patches, and hollow dashed polygons are "buffer" patches outside the study area. Barriers to dispersal (interstate highways, urban areas, etc.) are shown in black. Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.



Figure 1.2. Prioritization of patch and edge protection according to network type (genetic or demographic) and network metric used to rank features (ECP = effectively connected pairs, a measure of short-term network connectivity; MWC = mean weighted closeness, a measure of long-term connectivity). Black circles and lines represent existing patches and corridors included in the prioritization analysis; circle size and line width are inversely proportional to rank (larger circles and wider lines are more important patches and corridors to protect). White circles and dashed lines represent "buffer" patches and associated corridors (not ranked). Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.

# PREDICTING DIET QUALITY AND GENETIC DIVERSITY OF A DESERT-ADAPTED UNGULATE WITH NDVI

Tyler G. Creech, Clinton W. Epps, Ryan J. Monello, and John D. Wehausen

Journal of Arid Environments Elsevier Ltd., Stover Court, Bampfylde Street, Exeter, Devon, EX1 2AH, UK Volume 127, pp. 160-170 (2016)

# CHAPTER 2: PREDICTING DIET QUALITY AND GENETIC DIVERSITY OF A DESERT-ADAPTED UNGULATE WITH NDVI

Tyler G. Creech<sup>1</sup>, Clinton W. Epps<sup>1</sup>, Ryan J. Monello<sup>2</sup>, and John D. Wehausen<sup>3</sup>

<sup>1</sup>Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA <sup>2</sup> National Park Service, Biological Resource Management Division, Fort Collins, CO, USA

<sup>3</sup> White Mountain Research Center, University of California, Bishop, CA, USA

## ABSTRACT

Diet quality influences ungulate population dynamics but is difficult to measure at fine temporal or spatial resolution using field-intensive methods such as fecal nitrogen (FN). Increasingly, the remotely sensed vegetation index NDVI is used to represent potential ungulate diet quality, but NDVI's relationship with diet quality has yet to be examined for herbivores in desert environments. We evaluated how strongly NDVI was associated with diet quality of desert bighorn sheep (Ovis canadensis nelsoni) in the Mojave Desert using FN data from multiple years and populations. We considered effects of temporal resolution, geographic variability, and NDVI spatial summary statistic on the NDVI-diet quality relationship. NDVI was more reliably associated with diet quality over the entire growing season than with instantaneous diet quality for a population. NDVI was also positively associated with population genetic diversity, a proxy for long-term, populationlevel effects of diet quality. We conclude that NDVI is a useful diet quality indicator for Mojave Desert bighorn sheep and potentially other desert ungulates. However, it may not reliably track diet quality if NDVI data are too spatially coarse to detect microhabitats providing high-quality forage, or if diet is strongly influenced by forage items that are weakly correlated with landscape greenness.

#### **INTRODUCTION**

Diet quality has an important influence on the population dynamics of ungulates. Many studies have demonstrated the link between diet quality and individual body mass or body condition, which in turn affect survival and reproduction rates (Parker et al. 2009).

The nutritional quality of ungulate diets depends on the nutrient content of available forage species, which frequently varies spatially and temporally (Albon and Langvatn 1992; Festa-Bianchet 1988; McNaughton 1990). This variation largely reflects changes in plant phenology and is particularly evident in arid environments where precipitation is scant and geographically variable with a strong stochastic element (Bender 1982; Noy-Meir 1973), leading to pulses in forage growth and diet quality that can vary greatly in space and time. Accurately characterizing diet quality of ungulate populations in such environments may require sampling over broad areas at relatively fine spatial resolution (e.g., tens to hundreds of meters) and temporal resolution (e.g., days to weeks) to account for this heterogeneity; infrequent sampling may fail to capture pulses in diet quality that drive ungulate population dynamics, and geographically sparse sampling may fail to include localized hotspots of high forage quality.

Traditional methods of measuring diet quality limit researchers' ability to simultaneously maximize temporal and spatial resolution of diet quality sampling. Methods that assess diet quality by analyzing diet composition and nutrient content of forage plants can be too data-intensive to allow the development of data sets large enough to investigate temporal and spatial variation. Fecal indices of diet quality (most commonly fecal nitrogen, FN) have gained widespread acceptance as measures of ungulate diet quality (Leslie et al. 2008) and provide an indirect measure of diet quality at a much lower cost and time investment. Wehausen (1995) elucidated a causal mechanism that linked percent FN and apparent digestibility in a curvilinear relationship that was corroborated by data from domestic sheep and cattle, making FN a potentially meaningful index of diet quality for some ungulates. Yet, fecal indices still require extensive field sampling that limits the spatial and temporal extent and resolution for most studies.

The relationship between plant phenology and nutrient quality of herbivore diets has led to the use of remotely sensed vegetation indices such as the Normalized Difference Vegetation Index (NDVI) as alternative measures that may track ungulate diet quality. NDVI is a measure of vegetation greenness, based on reflectance in the red (RED) and near-infrared (NIR) regions of the electromagnetic spectrum, and is correlated with several variables that appear to be relevant to ungulate diet quantity and quality, including net primary productivity, plant biomass, and leaf area index (Pettorelli et al. 2011). It offers several advantages over other diet quality methods, including fine spatial and temporal resolution, global coverage, data available as far back as 1981 from the Landsat program, typically low (or no) data acquisition cost, and perhaps most significantly, no field sampling or laboratory analysis once validated. These characteristics make NDVI a potentially powerful tool for examining diet quality at higher resolution and over longer time periods and larger spatial extents than would be possible with traditional field-based methods, thereby offering excellent opportunities for long-term monitoring. NDVI is not without limitations, however: it does not directly quantify any biological variable, and factors such as the scale of imagery (Teillet et al. 1997), atmospheric conditions (Kaufman and Tanre 1992), and differences in soil type (Huete and Tucker 1991) can affect its relationship to biological variables.

NDVI is increasingly used as a proxy for diet quality in studies of ungulate populations, and has been related to individual- and population-level characteristics such as body condition (Ryan et al. 2012), body mass (Herfindal et al. 2006; Mysterud et al. 2008), conception rate (Rasmussen et al. 2006; Trimble et al. 2009), and breeding phenology (Wittemyer et al. 2007). However, the relationship between NDVI and diet quality may differ among species and environments, so it is critical to verify and elucidate the details of this relationship before applying NDVI as a diet quality indicator in new situations. Only a few studies have related NDVI to empirical measures of ungulate diet quality such as FN: Hamel et al. (2009) found that NDVI predicted yearly variation in the timing of peak fecal crude protein for mountain goats (*Oreamnos americanus*) and Rocky Mountain bighorn sheep (*Ovis canadensis canadensis*) in a Canadian alpine ecosystem; Ryan et al. (2012) found NDVI to be a positive predictor of FN for African buffalo (*Syncerus caffer*) in a South African savanna ecosystem; and Lendrum et al. (2014) observed corresponding increases in NDVI and FN for mule deer (*Odocoileus hemionus*) during spring migration in northwestern Colorado, USA.

Here, we use a long-term FN dataset to evaluate the association between NDVI and diet quality for an ungulate adapted to arid environments, the desert bighorn sheep (*Ovis canadensis nelsoni*), in the Mojave Desert, USA. FN has served well as an indicator of bighorn sheep diet quality in previous studies (Blanchard et al. 2003; Irwin et

al. 1993; Rubin et al. 2002; Wehausen 1992, 2005), but NDVI could greatly expand research opportunities if found to be a suitable proxy for diet quality. The Mojave Desert is characterized by relatively widespread winter precipitation and spatially heterogeneous summer monsoon thunderstorms (Bender 1982). Temperature patterns create a temporally predictable winter-spring growing season, but inter-annual and geographic variation in the timing and amount of precipitation results in large variation in forage growth and nutrient availability within the growing season (Wehausen 2005). Bighorn sheep populations inhabit discrete and often isolated mountain ranges separated by broad valleys that are less hospitable (Bleich et al. 1990; Schwartz et al. 1986), limiting their opportunity to shift to areas supporting higher diet quality when there is intermountain variation in nutrient availability. Previous research in this system has shown that diet quality is strongly associated with reproductive success, as measured by lamb:ewe ratios (Wehausen 2005). Additionally, populations inhabiting mountain ranges with lower maximum elevation and precipitation (where diet is presumably poorer) have higher extinction probability (Epps et al. 2004) and lower genetic diversity (Epps et al. 2006) than those in mountain ranges with higher maximum elevation and precipitation. These findings, along with forecasted increases in temperature and aridity for the region (Bernstein et al. 2008; Seager et al. 2007), suggest that more widespread data on diet quality in the region could aid in both retrospective and prospective analyses of bighorn sheep population dynamics.

The ability to assess the relationship between NDVI and population dynamics is hampered by a lack of demographic data such as population size estimates or recruitment rates for most Mojave Desert bighorn sheep populations. However, genetic diversity has been characterized for most populations in the region and may serve as a proxy for longterm population dynamics. Genetic diversity measures the extent of heritable variation in a population or species, and differences in neutral (i.e., non-expressed) genetic diversity among populations are a function of both gene flow (the amount of dispersal and subsequent reproduction between populations, influenced by population connectivity) and genetic drift (the random loss of alleles that occurs faster in smaller populations). After accounting for differences in connectivity, the remaining variation in genetic diversity among populations should primarily reflect population demographic history: populations that remain consistently large through time will have higher genetic diversity than smaller and less stable populations. This is a fundamental prediction of population genetic theory and is supported by a large body of empirical research (Crow and Kimura 1970; Frankham 1996; Soulé 1976). The effect of population size and stability on genetic diversity should be especially acute in metapopulations, where periodic extinctions and recolonizations by a small number of individuals can dramatically reduce genetic diversity via inbreeding, random genetic drift, and founder effects (Frankham et al. 2002; Pannell and Charlesworth 2000).

We use fecal nitrogen data from five populations and genetic data from 22 bighorn sheep populations in the Mojave Desert to test four hypotheses about the relationships between NDVI, diet quality, and genetic diversity of Mojave Desert bighorn sheep that may also be relevant to many other ungulate species and regions: (1) The relationship between NDVI and diet quality differs for populations occupying different habitat patches. Previous research suggests that populations of a species in different locations may exhibit different relationships between NDVI and diet quality (Martinez-Jauregui et al. 2009). For instance, two habitat patches could have similar NDVI values but contain different forage plant species and consequently support different levels of ungulate diet quality. (2) NDVI is a better predictor of diet quality at the temporal resolution of the entire growing season than at the resolution of individual samples representing instantaneous diet quality on a given day. The location of bighorn sheep within a patch may vary between areas of higher and lower forage quality on a daily basis, such that a patch-level summary statistic of NDVI on any particular day may not accurately represent the actual diet quality experienced by bighorn sheep. NDVI summarized at an intermediate temporal resolution, such as a growing season, could better reflect diet quality by integrating daily fluctuations over a longer, critical time period. (3) At a given point in time, diet quality is more highly correlated with the highest NDVI within a habitat patch than with average NDVI within the patch. Patch-level summaries of NDVI values should reflect the degree to which animals find and utilize areas with the best forage, so measures of average NDVI within an area may poorly represent diet quality if NDVI is spatially heterogeneous and animals preferentially feed in locations with the highest NDVI values. (4) Long-term NDVI conditions in a habitat

patch are positively associated with genetic diversity of the population occupying that patch. If NDVI is strongly associated with diet quality at the growing-season level, it may be possible to use NDVI to evaluate the long-term impact of habitat patches' forage quality on bighorn sheep populations, with genetic diversity serving as a proxy for demographic data.

#### **METHODS**

#### Study area

Our study area encompassed 23 currently occupied habitat patches in the Mojave Desert of southern California and Nevada (Fig. 2.1) for which bighorn sheep genetic data (Epps et al. 2006; Epps et al. 2005) and/or FN data were available. The study area includes transitional environments that represent varying mixtures of Mojave Desert characteristics and Great Basin Desert (to the north) or Sonoran Desert (to the south and southeast) characteristics. Variation in precipitation and temperature regimes, and resulting vegetation communities, is largely driven by elevation, which ranges from approximately sea level to 2500 m. Mean annual precipitation is 13.6 cm, but increases with elevation and varies across other geographic gradients. While most precipitation is derived from soaking winter rain storms, summer storms account for at least a third of the annual precipitation (Bender 1982). Mean annual temperature is 19.9°C and declines with elevation. Daily temperature range can be as much as 25°C (Bender 1982). Vegetation includes shrubs, trees, succulents, and perennial and annual herbs, but is generally sparse; Wallace and Thomas (2008) estimated that the majority of the Mojave Desert has less than 20 percent cover. Shrubs are the dominant plant form and important shrub species include creosote bush (Larrea tridentata), catclaw acacia (Acacia greggii), burrobush (Ambrosia dumosa), and brittlebush (Encelia farinosa) at lower elevations, and Mormon tea (*Ephedra spp.*), blackbrush (*Coleogyne ramosissima*), and sagebrush (*Artemisia* spp.) at higher elevations. Perennial grasses are largely absent at lower elevations and increase in cover with elevation; important species are big galleta grass (Hilaria rigida), desert needle grass (*Stipa speciosa*), and Indian ricegrass (*Achnatherum hymenoides*). Tree species include Joshua tree (Yucca brevifolia), juniper (Juniperus californica), and

pinyon pine (*Pinus spp*.). Annuals include both winter and summer annual forb and grass species that grow and flower in response to seasonal rainfall (Bender 1982).

Bighorn sheep habitat in the study area is defined by surface water availability and by the presence of steep, rocky slopes (escape terrain), which occurs mostly in small and discrete mountain ranges within the region; accordingly, patch boundaries were delineated along the margins of mountain ranges where steep slopes transition to flat valleys, using 10% slope as a cutoff as in Epps et al. (2007). Habitat patches ranged in size from 79 to 637 square kilometers (Table H.1). Because movement between habitat patches is infrequent, each population of Mojave Desert bighorn sheep corresponds to a single habitat patch, and we use the terms "patch" and "population" interchangeably.

# NDVI data

We used 8-day composite, 250-m resolution NDVI data from the Moderate Resolution Imaging Spectroradiometer (MODIS). Pre-processed data for the years 2000 through 2011 (MOD09Q1, Level 3, Collection 5, tile h08v05) were obtained from MODIS for the North American Carbon Program (MODIS-for-NACP, http://accweb.nascom.nasa.gov; Gao et al. 2008). Other satellite data offer finer spatial resolution, most notably Landsat Thematic Mapper with 30-m pixels, but we chose MODIS data for several reasons. First, the finer temporal resolution of MODIS data is an important advantage in our study system, where large changes in forage phenology can occur over short time periods. MODIS collects an image of a location every 1-2 days, and the composite dataset we used included the best-quality pixel from every 8-day period. In contrast, Landsat collects an image of a location only once every 16 days, and if conditions are poor at the time of image acquisition (e.g., clouds present), then the time between useable images could be more than a month. Second, Sesnie et al. (2011) found MODIS-derived NDVI to be less sensitive to sun angle and terrain effects when estimating forage phenology in desert bighorn sheep habitat, although a terrain illumination correction for Landsat is now available (Tan et al. 2013) and may negate this advantage of MODIS. Lastly, the preprocessing and accessibility of the MODIS-for-NACP data make them more user-friendly for biologists with limited experience working with remotely sensed data.

We used ArcGIS 10.0 (ESRI 2010) to calculate three summary statistics from the NDVI values of all pixels with center points within the boundary of each patch for each

8-day composite image: 1) median NDVI, a hypothesized measure of the average forage quality within the patch; 2) maximum NDVI, which may better reflect diet quality if bighorn sheep tend to seek out the highest-quality forage within the patch; and 3) the 90<sup>th</sup> percentile of NDVI, which could represent weaker selection of highest-quality forage than maximum NDVI, and is more resistant than maximum NDVI to spuriously high values caused by measurement error.

#### Fecal nitrogen data

We used FN measurements for 275 samples collected from 5 populations (Marble Mountains, Old Dad Peak, Orocopia Mountains, South Bristol Mountains, and Sheephole Mountains) from 2000 through 2011, with varying sampling intensity among populations (Fig. H.1). Two populations, Marble Mountains and Old Dad Peak, were sampled at approximately monthly intervals during 2000-2011; samples from other populations were collected less frequently or during fewer years. Each sample was a composite of multiple subsamples (range = 1-14, mean = 5.9; Fig. H.2) from different fecal piles collected over < 7 days. Samples consisted of freshly deposited pellets, except for a small proportion  $(\sim 5\%)$  that were recent pellets (i.e., < 7 days old) that were back-dated to the estimated date of deposition on the basis of the condition of pellets and tracks. Equal amounts of fecal material from each subsample were combined to form the composite sample (Jenks et al. 1989). Sampling was focused in areas where most ewes in the population were located at that time of year in an attempt to best represent the ewe population, and sampling locations were mostly consistent from year to year. We could not verify that each subsample was from a different individual; however, individuals move over large areas each day during feeding and thereby individually integrate much of the variation in nutrient availability across the landscape.

Nitrogen content of composite samples was analyzed by the Wildlife Habitat and Nutrition Laboratory at Washington State University with the Kjeldahl method (Horwitz 1965) for samples from 2000-2004, and with the Dumas method of combustion (Helrich 1990) using a TruSpec C/N Analyzer (LECO Corp., St. Joseph, MI) for samples from 2005-2011. FN was measured on an ash-free basis to correct for variation in the amount of inorganic material within pellets, including dirt, which does not contribute to diet quality (Wehausen 1995). Ash-free FN values were log-transformed to make their relationship with digestibility linear (Wehausen 1995) and thus more biologically interpretable. Hereafter, we refer to log-transformed, ash-free fecal nitrogen simply as fecal nitrogen or FN.

#### **Relationship between NDVI and fecal nitrogen**

We examined the relationship between FN and NDVI at two temporal resolutions: the sample (essentially a snapshot in time) and the winter-spring primary growing season. We defined the growing season for each year as the period from October 1 of the previous year through June 30 of the stated year, during which the majority of precipitation in the Mojave Desert occurs and potentially initiates sustained plant growth (Beatley 1974), and when the greatest pulse in diet quality occurs for bighorn sheep in this region (Wehausen 2005).

#### Sample level

For each FN sample (n = 275) from each population (n = 5), we identified the NDVI image closest to the FN sample date (calculated as the mean of estimated subsample deposition dates), and used the median, maximum, and 90<sup>th</sup> percentile NDVI within with the appropriate habitat patch in those images as potential predictors of FN. Preliminary examination of the data revealed that linearity of the relationships between FN and each of the three NDVI summary statistics was improved by log-transforming values of all summary statistics (Figs. H.3, H.4). We also improved linearity by back-transforming FN to its original scale via exponentiation for the sample-level analysis; however, we also present results in terms of log-transformed FN because of its direct biological relationship to diet quality.

We calculated the Pearson correlation coefficient between FN and each NDVI summary statistic for each population to determine which correlated best with bighorn sheep diet quality. We conducted all further analyses with the summary statistic most highly correlated with FN for the majority of populations. Because FN data exhibited a clear pattern of serial autocorrelation within populations (Fig. 2.2), we fit linear models of the FN-NDVI relationship using generalized least squares with a Gaussian correlation structure to account for autocorrelation of residuals. Models were fit in R (R Development Core Team 2014) using the *nlme* package (Pinheiro et al. 2011). We constructed three linear models of the FN-NDVI relationship: a model including NDVI,

population, and their interaction as covariates, which allowed the FN-NDVI relationship to have different slopes and different intercepts among populations (*separate lines*); a model including NDVI and population, but no interaction, as covariates, which allowed only intercepts to differ among populations (*parallel lines*); and a model including only NDVI as a covariate, such that a single regression line was fit to all populations (*equal lines*). We used likelihood ratio tests to select the best-fitting model.

#### Season level

We used areas-under-the-curve to compare FN and NDVI over the yearly growing season (Oct. 1 – June 30, 273 days). FN was sampled for all or most of the months during the growing season from 2001 through 2011 for only two populations, Marble Mountains and Old Dad Peak (Fig. H.1), so this analysis was limited to 22 season-level FN observations (11 per population). We constructed growing-season FN curves for Marble Mountains and Old Dad Peak by fitting a piecewise polynomial spline (essentially a smooth curve connecting consecutive data points) to the series of monthly FN measurements for each population with the *splines* package in R (R Development Core Team 2014); in cases where FN samples were not available for every month of the growing season (Fig. H.1), we interpolated between the previous and subsequent monthly values when constructing curves. Similarly, we constructed growing-season NDVI curves by fitting splines through NDVI values (again, using the summary statistic most highly correlated with FN values from the sample-level analysis) from 8-day composite images within the growing season. We explored the FN-NDVI relationship at the season level by calculating the area under the growing-season FN curve (integrated FN, or IFN) and the area under the growing-season NDVI curve (integrated NDVI, or INDVI), excluding the portion of the year outside of the growing season. We log-transformed INDVI to make its relationship with IFN more linear. As in the sample-level analysis, we then fit three linear regression models that allowed the relationship between IFN and INDVI to differ between the two populations to varying degrees (i.e., separate, parallel, or equal lines). Because we observed no pattern of serial autocorrelation at the season level, we used ordinary least squares to fit linear regression models and extra-sum-of-squares F-tests to select the best-fitting model.

#### **Characteristics of FN and NDVI curves**

We calculated several statistics to measure how closely seasonal changes in NDVI tracked changes in FN in the Marble Mountains and Old Dad Peak patches. First, we calculated the difference in the date of peak NDVI and peak FN for each growing season. Second, we examined the percentage of IFN and INDVI associated with each month of the growing season by integrating FN and NDVI splines for each month individually, using the minimum FN or NDVI value observed during 2001-2011 growing seasons in each patch as a baseline level for integrations to maximize the signal:noise ratio. We calculated the mean monthly percentages and 95% confidence intervals for each month to describe how FN and NDVI were temporally distributed within the growing season and the degree of consistency between the FN and NDVI distributions.

Lastly, we examined the degree to which IFN and INDVI were influenced by two characteristics of the FN and NDVI curves: the maximum value reached during the growing season (i.e., peak height) and the duration above summer baseline level (i.e., peak width). We estimated baseline values of FN = 0.7 and median NDVI = 0.14 from the curves in Fig. 2.2, then calculated peak width for each growing season as the number of days between the closest points on either side of the peak date at which the spline dropped below the threshold value. We regressed IFN and INDVI against their respective peak heights and peak widths, and calculated the change in  $R^2$  associated with removing each of these explanatory variables from the regression model as an indicator of the relative influence of peak height and width on total area under the curve.

#### **Relationship between NDVI and genetic diversity**

We used existing genetic data (Epps et al. 2005) from 22 populations in the Mojave Desert (Fig. 2.1) to determine whether long-term NDVI of habitat patches was correlated with genetic diversity. Our genetic dataset included genotypes of 399 individuals at 14 microsatellite loci, representing 4 to 37 individuals per population. Details of genotyping procedures can be found in Epps et al. (2005). We used the program FSTAT (Goudet 2001) to calculate two common genetic diversity metrics for each population, expected heterozygosity ( $H_e$ ) and allelic richness ( $A_r$ ); we used rarefaction to correct  $A_r$  for variation in sample size among populations. To characterize long-term diet quality for these populations, we calculated INDVI of each patch for each growing season from 2001 through 2011 using the same method described for the season-level analysis in Section 2.4.2. We then calculated the median of yearly INDVI values for each patch during these 11 years. We used linear regression to estimate the association between NDVI and genetic diversity, with  $H_e$  or  $A_r$  as the response variable and median INDVI as the predictor variable. Because relationships between genetic indices and median INDVI were nonlinear and could not be made linear by logarithmic transformation, we fit quadratic linear regression models by adding a squared term for median INDVI.

We also included population connectivity as a predictor variable because genetic diversity can be strongly influenced by the gene flow; populations that are more connected to neighboring populations receive more new alleles via immigration, which counteracts the loss of genetic diversity that occurs through genetic drift. Previous research on the Mojave bighorn sheep metapopulation has demonstrated that genetic diversity is higher in populations that are separated from their neighbors by shorter distances (Epps et al. 2006) and that gene flow between populations decreases with distance and the presence of dispersal barriers such as interstate highways (Epps et al. 2005). We considered four network-based connectivity metrics from Creech et al. (2014) that describe connectivity of Mojave bighorn sheep populations at local or regional scales (Appendix A); however, we used only the connectivity metric with the highest correlation with  $A_r$  or  $H_e$  (Table H.2) in regression models because all connectivity metrics were highly correlated ( $r \ge 0.75$ ).

To determine whether NDVI or connectivity had greater influence on genetic diversity, we fit single-predictor models (i.e., only NDVI or only connectivity) in addition to our multiple linear regression model, and compared the explanatory power  $(R^2)$  of these single-factor models. We used extra-sum-of-squares F-tests to determine the best-fitting model for each genetic diversity index. Although habitat patch size is an important influence on population size (and potentially on genetic diversity) in many wildlife populations, research on the Mojave Desert bighorn metapopulation has shown no effect of patch size on genetic diversity (Epps et al. 2006; Epps et al. 2005), so we did not include patch size in our analysis. Because results could potentially be influenced by

spatial autocorrelation in genetic diversity (i.e., if nearby populations exhibit similar genetic diversity), we repeated the analysis using models that included a Gaussian spatial correlation structure, and compared the results to those from non-spatial models.

#### RESULTS

#### Sample-level FN versus NDVI

Median NDVI had a higher correlation coefficient with FN than did maximum NDVI or 90<sup>th</sup> percentile NDVI for three of five populations, and had a correlation coefficient that was within 2 percent of the most highly correlated summary statistic for the remaining two populations (Table H.3). The similarity between the three summary statistics in terms of their correlation with FN reflected the fact that the summary statistics themselves were highly correlated (Fig. H.5). We used the median as our NDVI summary statistic for the remainder of the analyses, and believe it was an appropriate indicator of average forage conditions because NDVI values within patches appeared approximately normally distributed (Fig. H.6).

We found a positive relationship (p < 0.001) between FN and median NDVI (Figs. 2.3, H.7). The best fitting model was the parallel lines model, in which the intercepts of the FN-NDVI relationships differed among populations (likelihood ratio = 42.91, p < 0.001) but the slopes did not (likelihood = 4.99, p = 0.289). However, it was clear that the equal lines model would be most appropriate if only considering the two long-term data sets (Marble Mountains and Old Dad Peak), as regression lines were nearly identical for these populations (Fig. 2.3). Pseudo<sup>1</sup>- $R^2$  for the best-fitting model was 0.42, suggesting that much of the variation in FN at the sample level remained unexplained.

#### Season-level FN versus NDVI

We found a highly significant (p < 0.001), positive relationship between IFN and INDVI over the full growing season for the Marble Mountains and Old Dad Peak populations (Fig. 2.4). There was no evidence that the parallel lines model ( $F_{1,19} = 0.139$ , p = 0.713) or separate lines model ( $F_{2,18} = 0.396$ , p = 0.679) fit the data better than the simpler equal

<sup>&</sup>lt;sup>1</sup> Traditional  $R^2$  cannot be calculated for generalized least squares models; pseudo  $R^2$  presented here is the squared correlation between observed and predicted dependent variable values, a measure of in-sample predictive ability that is similar to traditional  $R^2$  but not related to variance decomposition.

lines model, in which the relationship between FN and NDVI was the same for the two populations.  $R^2$  for this best-fitting equal lines model was 0.64, indicating that NDVI explained the majority of season-level variation in FN; thus, NDVI was a better predictor of diet quality at the season level than at the sample level.

### **Characteristics of FN and NDVI curves**

The peak magnitude and seasonal pattern of NDVI varied among years from 2000 through 2011, but the timing and relative magnitude of peaks in NDVI was similar among patches within the region (Fig. H.8). In the Marble Mountains and Old Dad Peak patches, peak FN typically occurred after peak NDVI (Fig. 2.2): peak NDVI preceded peak FN in 9 of 11 years in Marble Mountains and 8 of 11 years in Old Dad Peak, with mean lag times of 60 and 48 days, respectively. Mean monthly IFN percentages exceeded mean monthly INDVI percentages at the very beginning and during the last 2-3 months of the growing season, but the pattern was reversed during the middle of the growing season (approximately November through March; Fig. 2.5).

Both peak width and peak height were highly significant ( $p \le 0.002$ ) predictors of INDVI, but peak height explained a greater amount of variation in INDVI (Fig. H.9, Table 2.1). In contrast, peak width explained considerably more variation in IFN than peak height, which was not a statistically significant (p > 0.05) predictor of IFN (Fig. H.9, Table 2.1). We achieved qualitatively similar results using a range of threshold FN and NDVI values to define peak width, suggesting that the above conclusions were insensitive to the baseline values we selected.

#### Genetic diversity versus NDVI

The connectivity metric most strongly correlated with both  $A_r$  and  $H_e$ , demographic weighted closeness (Table H.2), was included as a predictor in regression models and log-transformed to make its relationships with genetic diversity indices linear.  $A_r$  and  $H_e$ were both positively related to growing-season median INDVI during 2001-2011, after accounting for connectivity (Table 2.2; Fig. H.6), and the relationship was slightly stronger for  $A_r$ . For both genetic diversity metrics, the multiple regression model including INDVI and connectivity as predictors was preferred over the INDVI-only model ( $A_r$ :  $F_{1,18} = 18.344$ , p < 0.001,  $H_e$ :  $F_{1,18} = 13.659$ , p = 0.002) and the connectivityonly model ( $A_r$ :  $F_{2,18} = 6.980$ , p = 0.006,  $H_e$ :  $F_{2,18} = 4.704$ , p = 0.023). The single-factor model with connectivity as the predictor had higher  $R^2$  than the model with median INDVI as the predictor for both genetic diversity indices (Table 2.2), suggesting that connectivity had a greater influence on genetic diversity than NDVI. Models accounting for possible spatial autocorrelation provided similar estimates and only marginally higher *p*-values (Table H.4).

#### DISCUSSION

#### Variation among habitat patches

The results of our sample-level analysis supported our hypothesis that FN-NDVI relationships differed among populations (Fig. 2.3). This result appeared to be mostly driven by the Orocopia Mountains population, which had considerably lower NDVI values than the other four populations considered, but comparable FN values. The Orocopia Mountains are the southernmost population by 60 km and have a climate more characteristic of the Sonoran Desert, where a larger proportion of annual precipitation arrives as summer rains (as opposed to dominant winter precipitation in the Mojave Desert). However, a previous FN analysis for a nearby Sonoran-influenced population (Turtle Mountains; Wehausen 2005), demonstrated a seasonal nutritional pattern similar to Mojave Desert populations, so major climatic differences probably do not explain the difference in the FN-NDVI relationship among patches. Differences among patches in the forage species consumed by bighorn sheep are a more likely explanation.

We did not observe differences in the FN-NDVI relationship among populations in our season-level analysis, but we compared only two populations that are separated by only 50 km and have similar precipitation patterns and plant communities. Hence, we could not verify whether NDVI would be appropriate for comparing seasonal diet quality between populations that are more geographically distant and thus more likely to exhibit important differences in plant communities and resulting forage quantity, quality, or phenology. On the whole, however, our results suggested that observed relationships between NDVI and diet quality may only apply locally, and spatial extrapolation is risky. It may be necessary to "recalibrate" the relationship between NDVI and diet quality by collecting FN samples when applying this method in new areas, which would require a significant initial investment but allow for efficient monitoring of local diet quality over the long term.

#### Effects of temporal resolution

We observed weaker relationships between NDVI and FN at the sample level than at the season level. Perhaps the simplest explanation for this finding is that individual FN samples included varying amounts of random error that balanced out when integrated at the season level. However, comparison of FN and NDVI curves suggested that a temporal mismatch in periods of peak NDVI and peak FN played a role in the weaker sample-level relationship. Peak FN typically lagged behind peak NDVI by 1-2 months, and the majority of the area under the curve was in the middle of the growing season for INDVI but shifted toward the end of the growing season for IFN (Fig. 2.5). The stronger relationship between FN and NDVI when the curves are integrated across the entire growing season suggests that early-season overestimates of diet quality by NDVI somewhat balance later season diet quality underestimates in years of better plant growth.

# **Drivers of NDVI and FN**

The difference we observed in the timing of peak FN and peak NDVI most likely reflects a difference in the types of plant growth to which FN and NDVI are most responsive. NDVI peaks in early to mid-spring (Fig. 2.2), coincident with the period of strongest green-up of annual plants in the Mojave Desert (Beatley 1974; Wallace and Thomas 2008). Field notes on forage phenology from the period of fecal sample collection (J. Wehausen, unpublished data) further support this premise: we documented widespread growth of annual plant species in the Marble and Old Dad Peak patches in all eight years in which NDVI exhibited a clear peak and in none of the four years in which NDVI remained near baseline levels throughout the growing season (Fig. 2.2). In contrast, while FN also responds to the early-season growth of annual and other cold tolerant species, it appears to respond most strongly to the appearance of highly digestible flowers of perennial species that become available later in the growing season. In the Marble Mountains and Old Dad Peak patches, flowers of the brittlebush shrub are an especially important food source in many years, as are the flowers of various other perennial species such as creosote bush, all of which elevate the nutrient level of bighorn diets during the second half of the growing season (J. Wehausen, personal observation). Thus, NDVI may track diet quality poorly when diets are composed primarily of flowers, perennial plants, or other items whose availability is not synchronized with peak green-up. These differences in nutrient intake tracked by FN and NDVI appear to explain why variation in IFN is mostly driven by the length of the growing season, while variation in INDVI instead reflects variation in peak value during the early green-up period.

We observed several instances in which growing-season pulses in FN were not accompanied by pulses in NDVI. For instance, during the 2002 and 2006 growing seasons in Marble Mountains and Old Dad Peak, there was virtually no increase in NDVI above summer baseline level, but FN still exhibited clear peaks in these growing seasons. This may reflect a reliance on foods not strongly linked with vegetation greenness (e.g., flowers of perennial species), which would have elevated FN in years of poor plant growth. Alternatively, the ability of bighorn sheep to maintain near-normal FN levels in growing seasons with low NDVI may have resulted from selective foraging in microhabitats such as washes where high quality forage was not detectable at the resolution of the NDVI data; this could have elevated FN before NDVI detected a change early in the growing season and at the end of the growing season.

#### Summarizing NDVI within a habitat patch

Median NDVI within a habitat patch was more strongly associated with FN than was 90<sup>th</sup> percentile or maximum NDVI for the majority of patches in our analysis, although correlations with FN for the three summary statistics were very similar in most cases. Given their mobility and nutrient-limited environment, we expected that bighorn sheep would selectively feed in portions of a habitat patch with the highest quality forage (and presumably the highest NDVI) and that this would result in stronger correlation with 90<sup>th</sup> percentile or maximum NDVI values. There are several plausible explanations for the slightly better performance of median NDVI. First, bighorn sheep may have integrated the fine-scale variation in nutrient availability by moving frequently and sampling multiple microhabitats. Such behavior could have resulted from conflicting habitat needs: dietary requirements are best met in areas of highest-quality forage, but the safest overnight bedding areas (around which bighorn sheep feed in the morning) are in steep terrain, often with poorer forage quality. Second, bighorn sheep could have fed over relatively limited areas of average forage quality; this explanation is plausible during late
spring and summer, when high temperatures can force bighorn sheep to remain close to water sources, but unlikely during other seasons when cooler weather affords greater flexibility in habitat use. Third, the 250-m resolution of our NDVI data may have been too coarse to distinguish microhabitats that provide high-quality forage within pixels of lower average quality. This lack of resolution is consistent with the peaks in FN that we observed during the growing season in years when NDVI remained at low levels throughout the year in the Marble Mountains and Old Dad Peak patches (e.g., 2002, 2006, and 2007 in Fig. 2.2).

#### NDVI and genetic diversity

We found evidence for an association between NDVI and genetic diversity of bighorn sheep populations. NDVI was significantly associated with both  $A_r$  and  $H_e$  of bighorn sheep populations, although to a lesser degree with the latter. Allelic richness tends to respond more quickly to population bottlenecks and other fluctuations than  $H_e$  when populations sizes are small (Leberg 2002), as is the case with desert bighorn sheep (e.g., Epps et al. 2006). Genetic diversity indices had a stronger association with connectivity than with NDVI (Table 2.2), but this may have been influenced by limitations of our analysis: the duration of our NDVI data may not have been long enough to fully characterize the long-term average and variability of NDVI in habitat patches, and our assumption that recent NDVI was representative of longer-term NDVI may not have been warranted given regional climate change.

# Saturation effect of NDVI

Results from all three temporal scales (sample, growing season, long-term) revealed a pattern of diminishing returns at the upper range of observed NDVI values, whereby further increases in NDVI were associated with negligible increases in diet quality or genetic diversity. We used logarithmic transformations to make these relationships linear for our sample- and season-level analyses, but the saturating pattern implies that bighorn sheep are able to maximize their diet quality even at intermediate levels of NDVI. Differences among populations in our sample-level analysis also support this conclusion; for instance, bighorn sheep in the Orocopia Mountains population had FN levels similar to those in the Marble Mountains and Old Dad Peak populations despite occupying habitat with much lower median NDVI (Fig. 2.3). However, this pattern could also have

arisen if bighorn sheep in the Sonoran-influenced Orocopia Mountains were consuming browse species that were higher in phenolic compounds, which reduce protein digestion and inflate FN (Mould and Robbins 1981).

The genetic diversity analysis suggested that this saturation effect applies over longer temporal scales. A quadratic relationship fit the data best and implied that both  $A_r$ and  $H_e$  actually declined slightly with increasing median INDVI for approximately the highest third of the range of median INDVI values observed (Figs. 2.6, H.10). However, the small number of data points in this upper range made it difficult to conclude with high confidence that the relationship was quadratic rather than asymptotic. If bighorn sheep are able to maximize diet quality at intermediate NDVI, as suggested by results from all three temporal resolutions examined in this study, this could conceivably lessen the initial negative effects of climate change. Current climate models generally predict increasing temperatures and decreasing precipitation for the southwestern United States (Garfin et al. 2014), but increased aridity may not immediately decrease population persistence in patches that have relatively high NDVI at present, assuming that other climate-influenced factors such as drinking water availability are not limiting. Conversely, under the less likely scenario that precipitation in some areas increases, persistence probability of bighorn sheep populations may not increase if they have already maximized diet quality at current NDVI levels.

### Limitations

Despite the strongly significant season-level relationship we observed between FN and NDVI, confidence and prediction bands for this relationship (Fig. 2.4) suggest that care is needed when applying this model in a predictive context. The model appears to adequately distinguish predicted mean FN values (and presumably diet quality) at different NDVI values, as evidenced by the relatively narrow 95 percent confidence band. However, the much wider 95 percent prediction band indicates that it will be difficult to predict FN for any particular growing season and patch with very high confidence using NDVI. Managers will need to balance the ease and availability of NDVI data against its predictive limitations. For instance, knowing with 75 percent confidence that FN is higher in year x than year y (or in patch x than patch y) might provide sufficient information to be useful in some applications, and is within the limitations of our model

(Fig. 2.4); in other instances, if greater confidence is needed, MODIS-derived NDVI would not be an appropriate tool. Thus, NDVI is perhaps most appropriate as a coarselevel tool for comparing temporal or geographic variability in bighorn sheep diet quality. At a minimum, however, NDVI can distinguish between growing seasons of very high and very low diet quality (as indicated by FN) with a high level of confidence. Additional years of FN data collection would help to clarify the predictive limits of this relationship.

Several lines of evidence presented above suggest that our ability to predict diet quality was limited by the relatively coarse spatial resolution of the MODIS NDVI data we used. At 250-m resolution, a large fraction of each pixel in our satellite imagery consisted of bare soil or rock rather than vegetation, and we suspect that important microhabitats providing high quality forage were not captured at this resolution. However, the fact that we still observed a strong relationship between FN and NDVI, with seasonal peaks in NDVI corresponding to vegetation green-up, demonstrates that some signal of vegetation was nevertheless present in our NDVI data. This is consistent with many previous studies (e.g., Dall'Olmo and Karnieli 2002; De La Maza et al. 2009; Santin-Janin et al. 2009; Wallace and Thomas 2008; Wallace et al. 2008) that have successfully used NDVI data with 250-m or even coarser resolution to study vegetation characteristics in sparsely vegetated areas. Using satellite data of finer spatial resolution (e.g., Landsat TM) would likely improve our ability to accurately characterize diet quality around dates of image acquisition, but the accompanying loss of temporal resolution would compromise that ability to detect rapid shifts in diet quality that occur in the Mojave Desert following precipitation events.

In a recent study of white-tailed deer (*Odocoileus virginianus*), Montheith et al. (2014) found that FN of lactating females was lower than that of non-lactating females and males fed the same diet because lactating females had greater ability to extract nitrogen from forage. The applicability of this finding to other ungulate species has not been tested, but major differences exist between deer and desert bighorn sheep with respect to the structure of the digestive system and the characteristics of forage plants consumed (Krausman et al. 1993). This, plus the fact that virtually all of our FN samples were from ewes and most of these were lactating, leads us to believe that any bias introduced by this issue was minimal. Nonetheless, we recommend that researchers

record the sex and lactation status of sampled individuals whenever possible in order to quantify any bias and, if necessary, develop separate models of the FN-NDVI relationship for individuals of different sex and/or different lactation status.

# CONCLUSIONS

We have demonstrated that NDVI is a useful indicator of seasonal diet quality of desert bighorn sheep in the Mojave Desert, a finding that can help address the logistical challenges of acquiring diet quality data for bighorn populations in this region. Wildlife managers might use such data to identify habitat patches with more favorable forage conditions that should be a higher priority for conservation actions such as reintroductions, addition of artificial water sources, or land use protections; conversely, NDVI could be used to identify patches with poorer forage conditions that do not warrant expending conservation resources. Although we have explored its utility for desert bighorn sheep only, NDVI may also provide a useful diet quality indicator for other desert-adapted ungulates, particularly those that occupy relatively discrete habitat patches or have clearly defined foraging ranges.

Nevertheless, we caution that the convenience of NDVI should not overshadow its apparent limitations. Our analysis suggests that NDVI may fail to reliably track diet quality if: 1) the spatial resolution of NDVI data is too coarse to detect microhabitats providing high quality forage, or 2) diet is strongly influenced by high-quality forage items that are weakly correlated with greenness (e.g., flowers). Thus, a detailed knowledge of dietary habits is critical for assessing the utility of NDVI as a diet quality indicator. Wildlife managers and researchers should understand which forage plants (and plant parts) are utilized at different parts of the year, how they are distributed on the landscape, and how well NDVI reflects the availability and digestibility of these food sources. Finally, we recommend verifying the relationship between NDVI and diet quality with more direct measures such as fecal nitrogen before applying NDVI as a diet quality indicator for a new species or environment.

#### ACKNOWLEDGMENTS

We thank E. Fleishman for comments on the manuscript, L. Ganio for statistical advice, S. Sesnie for guidance on satellite data acquisition and processing, and B. Davitt for FN laboratory analyses. Funding for this research was provided by the Golden Gate Chapter of Safari Club International and by the National Park Service's Climate Change Response (PMIS 162673) and Natural Resources Condition Assessment (Cooperative Agreement H8C07080001) programs.

# LITERATURE CITED

- Albon S, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65(3):502-513
- Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55(4):856-863
- Bender GL (1982) Reference handbook on the deserts of North America. Greenwood Press, Westport, Connecticut
- Bernstein L, Pachauri RK, Reisinger A, Intergovernmental Panel on Climate Change (2008) Climate change 2007: synthesis report. IPCC, Geneva, Switzerland
- Blanchard P, Festa-Bianchet M, Gaillard J-M, Jorgenson JT (2003) A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. The Journal of Wildlife Management 67(3):477-484
- Bleich VC, Wehausen JD, Holl SA (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4(4):383-390
- Creech T, Epps C, Monello R, Wehausen J (2014) Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology 29(4):605-619
- Crow JF, Kimura M (1970) An Introduction to Population Genetics Theory. Harper and Row, New York.
- Dall'Olmo G, Karnieli A (2002) Monitoring phenological cycles of desert ecosystems using NDVI and LST data derived from NOAA-AVHRR imagery. International Journal of Remote Sensing 23(19):4055-4071
- De La Maza M, Lima M, Meserve PL, Gutierrez JR, Jaksic FM (2009) Primary production dynamics and climate variability: ecological consequences in semiarid Chile. Global Change Biology 15(5):1116-1126
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, Rechel JL (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, McCullough DR (2006) Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15(14):4295-4302

- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- ESRI (2010) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA
- Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75(4):580-586
- Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conservation Biology 10(6):1500-1508
- Frankham R, Ballou JD, Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press, Cambridge
- Gao F, Morisette JT, Wolfe RE, Ederer G, Pedelty J, Masuoka E, Myneni R, Tan B, Nightingale J (2008) An algorithm to produce temporally and spatially continuous MODIS-LAI time series. Geoscience and Remote Sensing Letters, IEEE 5(1):60-64
- Garfin G, Franco G, Blanco H, Comrie A, Gonzalez P, Piechota T, Smyth R, Waskom R (2014) Chapter 20: Southwest. In: Melillo JM, Richmond TC, Yohe GW (eds), Climate Change Impacts in the United States: the Third National Climate Assessment. U.S. Global Climate Change Research Program, Washington, D.C.
- Goudet J (2001) FSTAT, version 2.9.3, A program to estimate and test gene diversities and fixation indices. Lausanne University, Lausanne, Switzerland
- Hamel S, Garel M, Festa-Bianchet M, Gaillard J-M, Côté SD (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology46(3):582-589
- Helrich K (1990) Official Methods of Analysis of the Association of Official Analytical Chemists. The Association, Arlington, VA
- Herfindal I, Solberg E, Sæther B-E, Høgda K, Andersen R (2006) Environmental phenology and geographical gradients in moose body mass. Oecologia 150(2):213-224
- Horwitz W (1965) Official Methods of Analysis of the Association of Official Agricultural Chemists. The Association, Washington, DC
- Huete A, Tucker C (1991) Investigation of soil influences in AVHRR red and nearinfrared vegetation index imagery. International Journal of Remote Sensing 12(6):1223-1242
- Irwin LL, Cook JG, McWhirter DE, Smith SG, Arnett EB (1993) Assessing winter dietary quality in bighorn sheep via fecal nitrogen. Journal of Wildlife Management 57(2):413-421
- Jenks JA, Leslie Jr DM, Lochmiller RL, Melchiors MA, Warde WD (1989) Effect of compositing samples on analysis of fecal nitrogen. Journal of Wildlife Management 53(1):213-215

- Kaufman YJ, Tanre D (1992) Atmospherically resistant vegetation index (ARVI) for EOS-MODIS. Geoscience and Remote Sensing, IEEE Transactions on 30(2):261-270
- Krausman PR, Wehausen JD, Wallace MC, Etchberger RC (1993) Rumen characteristics of desert races of mountain sheep and desert mule deer. The Southwestern Naturalist 38( 2):172-174
- Leberg P (2002) Estimating allelic richness: effects of sample size and bottlenecks. Molecular Ecology 11(11):2445-2449
- Lendrum PE, Anderson CR, Monteith KL, Jenks JA, Bowyer RT (2014) Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. Mammalian Biology-Zeitschrift für Säugetierkunde 79(6):369-375
- Leslie DM, Bowyer RT, Jenks JA (2008) Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management 72(6):1420-1433
- Martinez-Jauregui M, San Miguel-Ayanz A, Mysterud A, Rodriguez-Vigal C, Clutton-Brock T, Langvatn R, Coulson T (2009) Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? Global Change Biology 15(7):1727-1738
- McNaughton SJ (1990) Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345(6276):613-615
- Monteith KB, Monteith KL, Bowyer RT, Leslie DM, Jenks JA (2014) Reproductive effects on fecal nitrogen as an index of diet quality: an experimental assessment. Journal of Mammalogy 95(2):301-310
- Mould ED, Robbins CT (1981) Nitrogen metabolism in elk. Journal of Wildlife Management 45(2):323-334
- Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363(1501):2357-2366
- Noy-Meir I (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4(1):25-51
- Pannell JR, Charlesworth B (2000) Effects of metapopulation processes on measures of genetic diversity. Philosophical Transactions of the Royal Society B: Biological Sciences 355(1404):1851-1864
- Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Functional Ecology 23(1):57-69
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, Kausrud K (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46(1):15-27
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: Linear and Nonlinear Mixed Effects Models.
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rasmussen HB, Wittemyer G, Douglas-Hamilton I (2006) Predicting time-specific changes in demographic processes using remote-sensing data. Journal of Applied Ecology 43(2):366-376

- Rubin ES, Boyce WM, Stermer CJ, Torres SG (2002) Bighorn sheep habitat use and selection near an urban environment. Biological Conservation 104(2):251-263
- Ryan SJ, Cross PC, Winnie J, Hay C, Bowers J, Getz WM (2012) The utility of normalized difference vegetation index for predicting African buffalo forage quality. Journal of Wildlife Management 76(7):1499-1508
- Santin-Janin H, Garel M, Chapuis J-L, Pontier D (2009) Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago. Polar biology 32(6):861-871
- Schwartz OA, Bleich VC, Holl SA (1986) Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. Biological Conservation 37(2):179-190
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316(5828):1181-1184
- Sesnie SE, Dickson BG, Rosenstock SS, Rundall JM (2011) A comparison of Landsat TM and MODIS vegetation indices for estimating forage phenology in desert bighorn sheep (*Ovis canadensis nelsoni*) habitat in the Sonoran Desert, USA. International Journal of Remote Sensing 33(1):276-286
- Soulé M (1976) Allozyme variation: its determinants in space and time. In: Ayala FJ (ed), Molecular Evolution. Sinauer Associates, Sunderland, MA
- Tan B, Masek JG, Wolfe R, Gao F, Huang C, Vermote EF, Sexton JO, Ederer G (2013) Improved forest change detection with terrain illumination corrected Landsat images. Remote Sensing of Environment 136(0):469-483
- Teillet PM, Staenz K, William DJ (1997) Effects of spectral, spatial, and radiometric characteristics on remote sensing vegetation indices of forested regions. Remote Sensing of Environment 61(1):139-149
- Trimble M, Ferreira S, Van Aarde R (2009) Drivers of megaherbivore demographic fluctuations: inference from elephants. Journal of Zoology 279(1):18-26
- Wallace CS, Thomas KA (2008) An annual plant growth proxy in the Mojave Desert using MODIS-EVI data. Sensors 8(12):7792-7808
- Wallace CS, Webb RH, Thomas KA (2008) Estimation of perennial vegetation cover distribution in the Mojave Desert using MODIS-EVI data. GIScience & Remote Sensing 45(2):167-187
- Wehausen J (1992)The role of precipitation and temperature in the winter range diet quality of mountain sheep of the Mount Baxter herd, Sierra Nevada. Biennial Symposium of the North American Wild Sheep and Goat Council 8:279-292
- Wehausen J (2005) Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. In: Goerrissen J (ed), Symposium Proceedings for the Sweeney Granite Mountains Desert Research Center 1978–2003; A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, CA
- Wehausen JD (1995) Fecal measures of diet quality in wild and domestic ruminants. The Journal of Wildlife Management 59(4):816-823
- Wittemyer G, Barner Rasmussen H, Douglas-Hamilton I (2007) Breeding phenology in relation to NDVI variability in free-ranging African elephant. Ecography 30(1):42-50

# **TABLES AND FIGURES**

Table 2.1.	Effects o	of peak	height an	d peak	width	of FN	and	NDV]	[ curves	on I	FN	and
INDVI, re	espectively	у.										

Response	Predictor(s)	$P^{\mathrm{a}}$	Model $R^2$	$\Delta R^{2b}$
IFN <sup>c</sup>	FN peak height	0.055	0.92	0.02
	NDVI peak height	<0.001	0.95	0.28
	NDVI peak width	0.001	0.95	0.28

<sup>a</sup> Significance from *F*-test of  $\beta$ =0 for given covariate <sup>b</sup> Change in model  $R^2$  when variable is removed from model <sup>c</sup> Integrated FN

<sup>d</sup> Integrated NDVI

Table 2.2.	Models	of relationsl	nip between	1 genetic	diversity	and lo	ng-term	NDVI	for 22
bighorn sh	neep pop	ulations in th	ne Mojave	Desert.					

Response	Predictor(s)	$P^{\mathrm{a}}$	Model $R^2$
$A_r$	median INDVI <sup>b</sup>	0.007	0.69
	(median INDVI) <sup>2</sup>	0.012	
	log(connectivity <sup>c</sup> )	< 0.001	
$A_r$	log(connectivity)	<0.001	0.45
$A_r$	median INDVI	0.153	0.38
	(median INDVI) <sup>2</sup>	0.263	
$H_e$	median INDVI	0.026	0.62
	(median INDVI) <sup>2</sup>	0.041	
	log(connectivity)	0.002	
$H_e$	log(connectivity)	0.001	0.42
$H_{e}$	median INDVI	0.243	0.34
	(median INDVI) <sup>2</sup>	0.385	

<sup>a</sup> Significance from *F*-test of  $\beta$ =0 for given covariate <sup>b</sup> Median of growing-season integrated NDVI values from 2001 through 2011

<sup>c</sup> Demographic weighted closeness (Appendix A), a network-based measure of population connectivity



Figure 2.1. Bighorn sheep populations and their associated habitat patches considered in this study. Filled dark gray polygons represent populations in which fecal nitrogen (FN) data were collected and used to analyze the relationship between diet quality and Normalized Difference Vegetation Index (NDVI). Unfilled polygons represent populations in which genetic data (but not FN data) were collected and used to analyze the relationship between genetic diversity and NDVI. Genetic data were also collected in all FN-sampled populations except the Sheephole Mountains. Patch abbreviations: CAD - Cady Mountains, CHE - Chemehuevi Mountains, CLI - Clipper Mountains, CSS -Clark Mountains/South Spring Range, ECH – East Chocolate Mountains, EMO – Eagle Mountains, GRA – Granite Mountains, IRO – Iron Mountains, KME – Kingston Mountains/Mesquite Range, LSB – Little San Bernardino Mountains, MAR – Marble Mountains, NOR – Newberry Mountains/Ord Mountains, OKM – Old Dad Peak/Kelso Mountains/Marl Mountains/Club Peak/Indian Spring, ORO - Orocopia Mountains, OWO - Old Woman Mountains, PCC - Piute Range/Castle Peaks/Castle Mountains, PRG -Palen Mountains/Riverside Granite Mountains, PRO – Providence Mountains, QUE – Queen Mountain, SBR – South Bristol Mountains, SHE – Sheephole Mountains, TUR – Turtle Mountains, WHA – Woods Mountains/Hackberry Mountains.



Figure 2.2. Median Normalized Difference Vegetation Index (NDVI) and fecal nitrogen (FN) for the Marble Mountains (top) and Old Dad Peak (bottom) populations. Tick marks on x-axis are placed at Jan. 1 of each year. Gray vertical bands show Oct. 1 – June 30 growing seasons. Horizontal black and gray lines show baseline levels of FN and NDVI, respectively, used to determine width of growing season peaks.



Figure 2.3. Relationship between fecal nitrogen and Normalized Difference Vegetation Index (NDVI) at the sample level for the Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE) bighorn sheep populations from 2000 through 2011. Regression lines are from the best-fitting model with equal slopes but different intercepts for the patches. Top panel shows relationship modeled in linear regression analysis: log-transformed NDVI, FN back-transformed to original scale via exponentiation. Bottom panel shows relationship that is most biologically interpretable: NDVI on original scale, FN logtransformed to be linearly related to apparent digestibility. Regression lines for MAR and OKM overlap in figure but are not identical. Individual plots for each population are in Fig. H.7.



Figure 2.4. Relationship between integrated fecal nitrogen (IFN) and log of integrated Normalized Difference Vegetation Index (INDVI) during the Oct.-June growing season for the Marble Mountains (MAR) and Old Dad Peak (OKM) habitat patches between 2001 and 2011. Regression line (solid line) is from the best-fitting model with equal slopes and intercepts for the patches. Dark-shaded region is the 95% pointwise confidence band; medium- and light-shaded regions are 75% and 95% pointwise prediction bands.



Figure 2.5. Mean monthly percentages of total growing season area-under-curve (INDVI or IFN) in the Marble Mountains (top panel) and Old Dad Peak (bottom panel) patches. Points and error bars show means and 95% confidence intervals, respectively, of monthly percentages from 2001 through 2011. N = 11 for each month.



Figure 2.6. Relationship between genetic diversity (expected heterozygosity  $[H_e]$  and allelic richness  $[A_r]$ ) and Normalized Difference Vegetation Index (NDVI) for 22 Mojave Desert populations. NDVI is calculated as the median of growing-season integrated NDVI from 2001 through 2011. Partial residual plot (Fig. H.10) suggests a decline in genetic diversity indices at highest INDVI values after accounting for connectivity.

# CHAPTER 3: SIMULATING THE SPREAD OF SELECTION-DRIVEN GENOTYPES USING LANDSCAPE RESISTANCE MODELS FOR DESERT BIGHORN SHEEP

Tyler G. Creech<sup>1</sup>, Clinton W. Epps<sup>1</sup>, Erin L. Landguth<sup>2</sup>, John D. Wehausen<sup>3</sup>, Rachel S. Crowhurst<sup>1</sup>, Brandon Holton<sup>4</sup>, and Ryan J. Monello<sup>5</sup>

<sup>1</sup> Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA <sup>2</sup> Computational Ecology Laboratory, Division of Biological Sciences, University of Montana, Missoula, MT, USA

<sup>3</sup> White Mountain Research Station, University of California, Bishop, CA, USA

<sup>4</sup> Grand Canyon National Park, National Park Service, Grand Canyon, AZ, USA

<sup>5</sup> Pacific Island Network, Inventory and Monitoring Program, National Park Service, Hawaii National Park, HI, USA

# ABSTRACT

Landscape genetic studies based on neutral genetic markers have contributed to our understanding of the influence of landscape composition and configuration on gene flow and genetic variation. However, the potential for species to adapt to changing landscapes will depend on how natural selection influences adaptive genetic variation. We demonstrate how landscape resistance models can be combined with genetic simulations incorporating natural selection to explore how the spread of adaptive variation is affected by landscape characteristics, using desert bighorn sheep (Ovis canadensis nelsoni) in three differing regions of the southwestern United States as an example. We conducted extensive genetic sampling and least-cost path modeling to optimize landscape resistance models independently for each region, and then simulated the spread of an adaptive allele favored by selection across each region. Optimized landscape resistance models differed between regions with respect to landscape variables included and their relationships to resistance, but the slope of terrain and the presence of water barriers and major roads had the greatest impacts on gene flow. Genetic simulations showed that differences among landscapes strongly influenced spread of adaptive genetic variation, with faster spread (1) in landscapes with more continuously distributed habitat and (2) when a pre-existing

allele (i.e., standing genetic variation) rather than a novel allele (i.e., mutation) served as the source of adaptive genetic variation. The combination of landscape resistance models and genetic simulations has broad conservation applications and can facilitate comparisons of adaptive potential within and between landscapes.

#### **INTRODUCTION**

The field of landscape genetics has greatly enhanced our understanding of the influence of landscape composition and configuration on gene flow and genetic variation of organisms (Sork and Waits 2010). The most common product of landscape genetic studies is the landscape resistance model, which represents the cost of movement, reduction in survival, or willingness of an animal to move through the environment as a function of landscape characteristics such as cover type, topography, or degree of anthropogenic disturbance (Zeller et al. 2012). Landscape resistance models are developed using neutral genetic markers, which are ideal for investigating demographic processes, such as gene flow, migration, and dispersal, because neutral variation is not influenced by selective forces that can lead to incorrect inferences about these processes (Holderegger et al. 2006). However, many of our most pressing questions about the effects of landscape characteristics on species and populations concern adaptive genetic variation – the ultimate driver of evolutionary potential – and understanding how landscape characteristics affect the potential for spread of adaptive variation is a pressing need in landscape genetics (Holderegger and Wagner 2008; Manel and Holderegger 2013). This need will only increase as unprecedented rates of habitat modification (Oakleaf et al. 2015) and climate change (Smith et al. 2015) force many species to adapt to novel environmental conditions. Additionally, rapid advances in next-generation sequencing technology are making it much easier to identify adaptive loci and explore genotype-environment associations (e.g., Jones et al. 2013).

Much of our understanding of how landscape characteristics could influence the spread of adaptive variation comes from theoretical models, such as those that explore effects of population subdivision on the rate or probability of fixation of a beneficial mutation. For instance, beneficial mutations spread at a slower rate in structured populations (Slatkin 1976) and reach fixation faster when demes are two-dimensionally structured than one-dimensionally structured (Hartfield 2012). Yet, theoretical models tend to rely on simplifying assumptions about the spatial arrangement of populations and the nature of migration between them (e.g., island, stepping-stone, or lattice models of population structure) that are rarely borne out in real life. Characteristics of the intervening landscape between individuals or populations (e.g., habitat configuration, presence of dispersal barriers) are well known to limit animal movement and gene flow and ultimately affect the amount and spatial pattern of genetic differentiation (Cushman et al. 2012; Epps et al. 2005; Keyghobadi et al. 2005; Shoemaker and Jaenike 1997); these characteristics must be taken into account when assessing how real landscapes influence adaptive variation.

Landscape resistance models based on neutral genetic variation can play an important role in this regard by providing realistic, empirically-supported backdrops for simulating the spread of adaptive genetic variation across landscapes. Individual-based, spatially-explicit genetic simulators now allow us to incorporate natural selection in the simulation of gene flow and demographic processes across resistant landscapes (e.g., Landguth et al. 2012; Rebaudo et al. 2013). With many species widely distributed across landscapes that vary dramatically with respect to these landscape characteristics, simulation-based comparisons within and among landscapes could help to identify portions of a species' range where adaptive alleles are likely to spread quickly and facilitate in-situ adaptation, or conversely, where spread of adaptive alleles is likely to be slow and assisted gene flow may be necessary. Here, we demonstrate this approach in one of the largest landscape genetic studies to date, using desert bighorn sheep (Ovis *canadensis nelsoni*) in the southwest United States. We genotype > 850 individuals at neutral markers from three landscapes that vary with respect to habitat configuration and factors influencing gene flow, optimize landscape resistance models independently for these regions, and use genetic simulations to determine how differences among landscapes affect the capacity for spread of adaptive genetic variation.

Desert bighorn sheep occupy some of the hottest and driest portions of the southwest U.S, and their distribution is strongly limited by availability of reliable surface water and steep terrain to allow escape from predators (Monson and Sumner 1980). Habitat configuration is highly variable across the subspecies' range - linear and relatively continuous in some areas, but patchy in other areas – and presents an opportunity to explore the effects of habitat configuration on gene flow and natural selection. Other landscape characteristics also vary substantially across the subspecies' range, including climate, vegetation, degree of anthropogenic development, and presence of major barriers to dispersal. Research on factors affecting gene flow or dispersal of desert bighorn sheep has been largely limited to a portion of the subspecies' range in southern California and Nevada (Epps et al. 2005; Epps et al. 2007), where landscape resistance models are currently being used to manage risks to connectivity from renewable energy development (U.S. Bureau of Land Management 2015).

Climate projection models predict increases in temperature and aridity in the southwest U.S. in coming decades (Garfin et al. 2014; Seager et al. 2013), which could negatively impact bighorn sheep through decreasing water and forage availability or increasing heat stress. Bighorn sheep populations in the Mojave Desert have higher extinction probability (Epps et al. 2004) and lower genetic diversity (Epps et al. 2006) in hotter, drier low-elevation habitat than in cooler, wetter high-elevation habitat. Unlike many species that can respond to local climate change by shifting their spatial distribution either latitudinally or altitudinally to remain within their "bioclimatic envelope" (Chen et al. 2011; Parmesan 2006; Walther et al. 2002), desert bighorn have limited ability to make such geographic shifts; they are habitat specialists that rely on steep and open escape terrain that often comprises a small percentage of the landscape and may be discontinuously distributed, and they typically already occupy the highest-elevation (i.e., wettest and coolest) portions of available habitat. Therefore, desert bighorn are likely to be strongly dependent on in-situ adaptation to deal with an increasingly inhospitable climate.

In this study, we explore two scenarios under which adaptive genetic variation could arise and spread throughout a region to facilitate climate change adaptation (hereafter, referred to simply as "scenarios"). In the first, a novel allele favored by selection is introduced at one location – for instance, via a mutation or the intentional translocation of individuals with a novel genotype – and subsequently spreads outward from this origin point (hereafter, the "novel allele" scenario). In the second scenario, an allele that is already present throughout the region at low frequency becomes favored by

selection due to a change in environmental conditions – for instance, a shift in climate regime – and subsequently increases in frequency throughout the region (hereafter, the "pre-existing allele" scenario). We simulate each of these scenarios (novel versus pre-existing allele) in three regions that differ with respect to habitat configuration and factors influencing landscape resistance for bighorn sheep, and we compare rates of adaptive allele spread among regions and scenarios.

#### METHODS

Methods for this study included the following major components: (1) collecting and genotyping DNA samples from individuals in three regions at neutral microsatellite loci, (2) developing a suite of candidate landscape resistance models that describe how landscape variables influence gene flow, (3) using genetic data and least-cost path modeling to test the fit of candidate resistance models and identify an optimal model for each region, (4) simulating the spread of an adaptive allele in each region during 100 years of gene flow influenced by landscape resistance, with mate selection and dispersal determined as probabilistic functions of cumulative cost across optimized regional resistance surfaces, and (5) comparing results among regions for three selection strengths and two initial spatial distributions of the adaptive allele. We discuss each component in detail below.

## Study area

This study considers desert bighorn sheep populations in three regions of the southwest U.S. that differ substantially in habitat configuration. The southern Mojave Desert region (hereafter, MOJA) of southeastern California and southern Nevada contains bighorn sheep habitat distributed in discrete mountain ranges within a matrix of less hospitable flats (Fig. 3.1A). Populations in this region exhibit metapopulation structure, in which patches are linked by infrequent dispersal events (Bleich et al. 1996; Schwartz et al. 1986). Human development within the region is limited, but three major interstate highways fragment the metapopulation, and ongoing renewable energy development threatens to further disrupt connectivity (Lovich and Ennen 2011). Two large protected areas, Mojave National Preserve and Joshua Tree National Park, are located within the region and are minimally impacted by human development.

The Grand Canyon region (hereafter, GRCA) in northern Arizona is dominated by the Colorado River flowing between Lake Mead and Lake Powell within Grand Canyon National Park (Fig. 3.1B). Bighorn sheep are confined to the rugged terrain within the Grand Canyon and side canyons and avoid the surrounding plateau areas with poor escape terrain and visibility. The Grand Canyon is 277 river miles long and 10 miles wide on average within Grand Canyon National Park, so bighorn sheep habitat is relatively linear. GRCA is bordered by Glen Canyon and Lake Mead National Recreation Areas and habitat is continuous, but for the purposes of this analysis we consider only the GRCA section, which is more linear than adjacent habitat. Preliminary genetic analyses indicate strong genetic differentiation of individuals on opposite sides of the Colorado River, and weak differentiation within each side as a function of distance (T. Creech, unpublished data). Very little human development and few anthropogenic dispersal barriers exist within GRCA.

The Death Valley region (hereafter, DEVA) of the northern Mojave Desert along the California-Nevada border is centered on Death Valley National Park. Bighorn sheep populations occupy habitat patches that are relatively discrete and separated by flat, arid valleys, but are generally larger and more linear than in MOJA (Fig. 3.1C); thus, DEVA represents an intermediate habitat configuration between MOJA and GRCA. Minimal human development and few anthropogenic dispersal barriers are present in the DEVA region.

#### Genetic data

We obtained DNA mainly via non-invasive sampling of fecal pellets, and from a small number of tissue and blood samples from live captures, hunter kills, or carcasses found in the field. We used both newly-collected samples (2011-2013) from this dissertation, and samples collected for previous studies. MOJA samples were collected during 2000-2004 (Epps et al. 2006; Epps et al. 2005), while DEVA samples were collected in two phases: during 2003-2010 (Jaeger and Wehausen 2012) and during 2011-2013 to include areas previously omitted. Sampling in MOJA and DEVA was conducted primarily around water sources where bighorn sheep congregate during summer months. GRCA samples were collected during 2011-2013, and most samples were collected along the Colorado River and associated side canyons, with additional samples collected along trails and at

observation points within the national park. UTM coordinates were recorded for all GRCA samples and for DEVA and MOJA samples collected after 2010, but only approximate locations (e.g., the name of a water source) were recorded for DEVA and MOJA samples from earlier sampling periods. We assigned coordinates to these earlier samples based on the geographic feature where they were collected, and added a random locational error of up to 300 m (via random draw from a uniform distribution) to each sample location to reflect uncertainty about sampling locations in these areas, and to avoid having many individuals occupying a single landscape cell in subsequent landscape resistance surfaces.

Samples were analyzed using similar protocols in three genetics labs, corresponding to the three sampling periods. Descriptions of genotyping protocols for the two earlier periods (2000-2004 and 2003-2010) can be found in Epps et al. (2005) and Jaeger and Wehausen (2012). We briefly describe the protocol for the most recent period (2011-2013) below, but provide a more detailed description of DNA extraction, polymerase chain reaction (PCR) conditions, genotype calling and screening, and locus characteristics in Appendix I. We using a modified AquaGenomic Stool and Soil protocol (MultiTarget Pharmaceuticals LLC, Colorado Springs, CO) to extract DNA from material scraped from the surface of fecal pellets. We genotyped samples at 16 dinucleotide microsatellite markers in three multiplex PCRs of 4-6 markers using a Qiagen Multiplex PCR kit (Qiagen, Valencia, CA). We used an ABI 3730 capillary sequencer (Applied Biosystems [ABI], Foster City, CA, USA) to visualize PCR products and GENEMAPPER (version 4.1; ABI) to score genotypes. Each sample was amplified in at least three replicate PCRs to generate consensus genotypes. We used CERVUS version 3.0.3 (Kalinowski et al. 2007) to identify duplicate genotypes and GIMLET version 1.3.3 (Valière 2002) to estimate genotyping error rates (false allele occurrence rate and allelic dropout rate). We used GENEPOP version 4.2 (Raymond and Rousset 1995) to test for deviations from linkage equilibrium and Hardy-Weinberg equilibrium.

# **Genetic distances**

We used the Bray-Curtis dissimilarity index (BC; Bray and Curtis 1957), equivalent to 1 minus the proportion of alleles shared between individuals, as a measure of interindividual genetic distance to use in optimizing the landscape resistance models. BC is strongly correlated with and has provided similar performance to other individual-level genetic distance metrics (e.g., Rousset's  $a_r$ , PCA-based genetic distance) in previous studies (Castillo et al. 2014; Cushman et al. 2006; Schwartz et al. 2009; Shirk et al. 2010). We generated pairwise matrices of inter-individual genetic distance for each study area using the *ecodist* package (Goslee and Urban 2007) in R (R Development Core Team 2014).

#### Landscape variables

We considered seven variables that may affect bighorn sheep movement across the landscape (see Table J.1 for information on geospatial data sources): (1) Slope. Bighorn sheep prefer steep slopes that serve as escape terrain from predators (Krausman et al. 1999). (2) Normalized Difference Vegetation Index (NDVI). This remotely-sensed measure of vegetation greenness is correlated with bighorn sheep diet quality (Creech et al. 2016; Hamel et al. 2009), and individuals could be more likely to move through areas offering better forage. We used a time-integrated NDVI (TIN) spatial dataset that estimates the total photosynthetic activity during the annual growing season. (3) Anthropogenic development. Bighorn sheep are intolerant of human activities in most cases (Valdez and Krausman 1999) and may avoid permanently developed areas (Monson and Sumner 1980). (4) Major roads. Roads can be strong barriers to bighorn dispersal (Epps et al. 2005). Genetic analyses (Epps et al. 2005; Epps et al. 2007) and anecdotal evidence suggest that four-lane and fenced highways are rarely crossed by bighorn, while smaller, unfenced highways and roads are crossed frequently; thus, we considered only four-lane or fenced highways to be major roads. (5) Distance to water. The availability of permanent water sources is a key limiting factor for bighorn sheep populations (Monson and Sumner 1980) and may influence individuals' ability or willingness to disperse through arid environments. We identified reliable water sources for bighorn sheep, including perennial streams, springs, seeps, lakes, reservoirs, and artificial guzzlers, and calculated the distance from each landscape cell to the nearest source. (6) Forested areas. Forested areas limit visibility and increase predation risk for bighorn sheep (Wilson et al. 1980). (7) Water barriers. Larger water features may serve as barriers to movement, as bighorn are thought to rarely cross high-volume rivers or reservoirs (e.g., Colorado River, Lake Powell). We used a combination of expert opinion, anecdotal evidence, and empirical evidence from radiocollar tracking and genetic data to identify water barriers in the region. We did not include the major roads variable in our analysis for the DEVA or GRCA regions, or the water barriers variable in our analysis for the DEVA region, because these features were not present in these regions, respectively.

Geospatial data layers ranged in spatial resolution from 30 m to 250 m cells, but needed to be combined in a single-resolution, multivariate resistance layer. We used the *raster* package (Hijmans 2014) in R to resample all layers to 3-arcsecond (approximately 100 m) cell resolution in order to meet computational limitations when calculating cost distances.

#### **Candidate univariate surfaces**

We used a combination of expert opinion and previous modeling studies to develop plausible alternative resistance parameterizations for each landscape variable to be tested with the genetic data. We included a large range of parameterizations to maximize the probability of bracketing the true resistance value (Tables K.1, K.2). For continuous variables (slope, NDVI, distance to water), we modeled several possible relationships with landscape resistance, including linear relationships and concave-up and concavedown non-linear relationships (i.e., monotonic relationships in which the rate of change in resistance varies across the range of landscape variable values; Fig. K.1). For slope, we also included Gaussian relationships (e.g., Cushman et al. 2006) in which resistance was lowest at some intermediate slope value and increased as the slope value moved away from the optimum (Fig. K.2), and breakpoint relationships in which slopes within an intermediate range were assigned a resistance value of 1, while slopes outside this range were assigned a single, higher resistance value. These relationships are plausible because shallow slopes increase predation risk and very steep slopes could be too difficult for bighorn sheep to negotiate.

For binary variables (anthropogenic development, major roads, forested areas, water barriers), we considered several possible ratios of resistance for the two types of cells (e.g., natural versus converted, or forested versus non-forested) by assigning the less resistant cell type a resistance value of 1 and assigning a range of resistance values for the more resistant cell type based on expert opinion. Additional detail on alternative parameterizations for each variable is in Appendix K.

# **Cost distances**

For each resistance surface, we used the *gdistance* package (van Etten 2012) in R to generate a pairwise matrix of inter-individual cost distances, calculated as the accumulated cost along the least-cost path (Adriaensen et al. 2003) between sample locations for pairs of individuals. We used an individual-based rather than population-based approach for relating genetic distance and cost distance because it did not require defining populations a priori, and was therefore more appropriate in areas where bighorn sheep were continuously distributed (e.g., Grand Canyon). Recent studies have supported the use of individual-based approaches in landscape genetics (Bolliger et al. 2014; Landguth et al. 2010), even in cases where discrete populations exist (Prunier et al. 2013).

# **Resistance surface optimization**

Mantel tests have been the standard approach for evaluating competing resistance surfaces in landscape genetic studies (Manel and Holderegger 2013), but there is mounting evidence that they may not be appropriate or reliable for such applications (Cushman et al. 2013b; Graves et al. 2013; Guillot and Rousset 2013; Kierepka and Latch 2014; Zeller et al. in review). We relied on an alternative approach that fits linear regression models using bootstrap sampling of independent pairs of individuals and has been successfully applied in several recent landscape genetic studies (Dudaniec et al. 2013; Dudaniec et al. 2015; Mehner et al. 2009; Rioux Paquette et al. 2014; Worthington Wilmer et al. 2008). We used a two-phased approach (Castillo et al. 2014) to optimize landscape resistance surfaces for each region: in the first phase, we tested sets of candidate resistance surfaces representing different resistance parameterizations of a single landscape variable and identified optimal univariate surfaces; in the second phase, we tested candidate multivariate surfaces including various subsets of the optimal univariate surfaces, as well as variants of the optimal univariate surfaces rescaled to have different maximum resistance values, and identified an optimal multivariate surface. This process was performed independently for each region, and we describe both phases in further detail below.

#### Univariate optimization

We used a pseudo-bootstrapping approach (Worthington Wilmer et al. 2008) to compare candidate resistance surfaces. This approach was similar to traditional linear regression, but accounted for the non-independence of pairwise data (in this case, genetic and cost distance matrices) by repeatedly selecting a random and independent subset of pairs from the dataset (i.e., each individual represented in only a single pairwise value). For each random subset, we fit a linear regression model of genetic distance as a function of cost distance for each candidate resistance surface and calculated Akaike Information Criterion (AIC). We slightly modified the procedure of Worthington Wilmer et al. (2008) by using a Mantel correlogram to estimate the Euclidean distance beyond which genetic distance and Euclidean distance were no longer correlated in each study region, and excluding all pairs separated by distances greater than this cutoff; the purpose of this step was to remove pairwise comparisons that did not contribute useful information on the relationship between gene flow and environmental characteristics because of very long distances between individuals. We performed 10,000 iterations of this procedure and used the median Akaike weight as our model selection criterion. A simple Euclidean distance surface (i.e., resistance surface with all cells having resistance value of 1) was included in the set of candidate surfaces for each variable to serve as a null model of isolation by distance (IBD). Because previous research has suggested that logtransforming cost-distances may improve linearity (Diniz-Filho et al. 2013; Graves et al. 2013; Zeller et al. *in review*), we fit each model with both unlogged and log-transformed cost distances, and retained the version with the higher model  $R^2$ .

## Multivariate optimization

We generated a candidate set of multivariate resistance models by summing resistance values (on a cell-wise basis) for all possible combinations of landscape variables, using the optimized univariate resistance surface for each variable. Any variable for which the optimized univariate surface did not perform better than IBD (i.e., did not have higher median Akaike weight) was excluded from all candidate multivariate resistance surfaces. To allow for the possibility of interactions between variables (i.e., changes in the optimal resistance model for one landscape variable when effects of other landscape variables are included in a multivariate resistance model), we also created candidate multivariate

models using univariate surfaces with the same shape of resistance curve as the best univariate surface, but with a different maximum resistance value. For instance, if the optimized univariate surface for the NDVI variable indicated a concave-down, negative relationship with a maximum resistance value of 50, we also created multivariate surfaces including concave-down, negative relationships with maximum resistance values of 10 and 100 for NDVI. We could not test all possible combinations of univariate models because allowing all univariate model parameters to vary for each landscape variable in multivariate models would have resulted in an excessive number of multivariate models. Other methods have been proposed to maximize the amount of the multivariate hypothesis space explored (e.g., Shirk et al. 2010), but all methods are constrained to some extent by computational limitations. We compared multivariate surfaces using the AIC approach described above. Because four or fewer landscape variables were more informative than the null model of IBD in each region, the number of multivariate models remained reasonable.

#### Simulation of adaptive allele spread

After identifying the best landscape resistance model for each study region using landscape genetic analysis of neutral markers, we used the computer program CDPOP v1.2 (Landguth and Cushman 2010) to simulate gene flow and natural selection in each of our study regions. CDPOP simulates dispersal and mating of individuals across a landscape resistance surface, allowing the user to define the initial genetic structure, spatial distribution of individuals, dispersal characteristics, and life history traits of the population. Natural selection is incorporated by allowing offspring mortality rate to vary as a function of individual genotype linked to environmental associations. We simulated selection at a single biallelic locus with an adaptive allele *A* and a non-adaptive allele *a*. We tested three different strengths of selection for the adaptive allele: a 10 percent ("weak selection"), 20 percent ("moderate selection"), or 30 percent ("strong selection") increase in offspring survival of the *AA* genotype relative to the *aa* genotype. We assumed additive dominance, whereby survival of the *Aa* genotype was intermediate (h=0.5) to the two homozygotes.

# Initializing individual locations and genotypes for simulation

We used maps of occupied desert bighorn sheep habitat provided by state wildlife agencies to assign individual locations, which remain fixed throughout simulations in CDPOP. Individuals were randomly placed within occupied habitat at a constant density of 0.2 individuals/km<sup>2</sup> in each region, resulting in 1,684 individuals for DEVA, 624 for GRCA, and 1,576 simulated individuals for MOJA. We arrived at this density by summing population size estimates for the MOJA and DEVA regions (based on the most recent available information, e.g., Epps et al. 2003) and dividing by the total area of occupied habitat within these two regions; a population estimate was unavailable for GRCA, so we assumed that the average bighorn sheep density in the other regions was a suitable estimate for GRCA. The assumption of constant density of individuals within and across regions was preferable to using actual population sizes because (1) population information was unavailable or outdated in many areas; (2) bighorn sheep population sizes can change dramatically over short time scales, especially in metapopulation systems such as the Mojave Desert or in the event of a disease outbreak, so current population estimates may only remain accurate for a short portion of the simulation time frame; and (3) we wanted to investigate the effects of differences in landscape configuration and resistance among regions without the variation introduced by differences in local population density.

For the novel allele scenario, we initialized genotypes with allele frequencies of 0.01 and 0.99 for the adaptive (*A*) and non-adaptive (*a*) alleles, respectively, in each regional population. We selected a single individual near the center of each region and identified the closest two percent of neighboring individuals in the landscape, based on cost distance. Among this subset of individuals, we randomly assigned half of the pooled alleles to be the *A* allele, and all remaining alleles within the region to be the *a* allele, creating a small cluster of *AA*, *Aa* and *aa* genotypes at Hardy-Weinberg equilibrium frequencies within a regional population that was otherwise homozygous for the *aa* genotype. These clusters of adaptive alleles were approximately 15 km in diameter in all three regions, and spanned portions of two populations each in DEVA and MOJA, and a small portion of the single continuous population in GRCA. We used this cluster strategy rather than initializing simulations with a single copy of an adaptive allele, as would

occur immediately following a mutation, because a single allele would quickly be removed from the population by genetic drift in most cases, even when selection was strong. Thus, this scenario might exemplify examining spread of a local adaptation or variant. For the pre-existing allele scenario, simulating a change in selective coefficient for an allele already present at some frequency across the region, we initialized genotypes with regional allele frequencies of 0.05 and 0.95 for the *A* and *a* alleles, respectively, and each allele randomly distributed among individuals in the region.

#### Simulation parameters

We simulated gene flow for 100 years following the initiation of genotypes, with 50 Monte Carlo replicates for each combination of selection strength (none, weak, moderate, strong) and scenario (novel allele or pre-existing allele). Mating and dispersal movements followed an inverse-square function of cost distance. To standardize cost distances among regions, we added 2 to each cell value in the optimized DEVA resistance surface so that the cost value of the least resistant cell type was constant across regions; this was necessary because multivariate surfaces were created by summing three univariate surfaces with a minimum value of 1 for GRCA and MOJA, but only a single univariate surface for DEVA.

We first ran simulations with a maximum movement threshold of 534,861 cost units, the cost distance beyond which genetic distance and cost distance were no longer correlated within the GRCA region; this was the smallest of such estimates for the three regions, using the best multivariate resistance models to estimate cost distance. Because maximum dispersal distance of bighorn sheep has not been precisely estimated and could influence the relative rate of spread of adaptive alleles, we repeated all simulations with ½ the original dispersal threshold (267,430 cost-units) and twice the original dispersal threshold (1,069,722 cost units) to bracket a range of likely dispersal thresholds; we hereafter refer to these threshold values as "low", "medium", and "high" dispersal thresholds. These cost distance thresholds correspond to Euclidean distances ranging between 2.4 and 13.6 km if individuals traveled through average-resistance terrain in each region; however, actual distances traveled in simulations could be much further than this because we assumed individuals traveled along least-cost paths. We allowed males but not females to mate with replacement in order to approximate the polygynous mating system of bighorn sheep. The population included 17 age classes, with age-specific mortality and fecundity rates estimated from the literature (Berger 1982; Krausman et al. 1999; Monson and Sumner 1980; Rubin et al. 2002; Schaeffer et al. 2000). Each mating event resulted in a single offspring, as twinning is rare in bighorn sheep (Geist 1971). We set mutation rate to zero, which is reasonable given the short time frame of the simulations (< 15 generations).

## Quantifying adaptive allele spread

We calculated the mean adaptive allele frequency (hereafter,  $f_A$ ) at every year by averaging results from the 50 MC replicates for each combination of selection strength and scenario. We plotted 95% confidence bands for  $f_A$  in each region as a function of time and compared confidence bands for differences in the rate of adaptive allele spread among regions.

#### RESULTS

# Genetic data

We genotyped 225 unique individuals from DEVA, 252 from GRCA, and 378 from MOJA. False allele occurrence rate was zero in all regions, and allelic dropout rate averaged 4.1 percent across loci and regions. We observed deviations from Hardy-Weinberg equilibrium or linkage equilibrium in a number of populations within the three regions; however, no locus (for HWE) or pair of loci (for LE) was consistently out of equilibrium across populations, suggesting that these deviations most likely resulted from population substructure rather than non-neutral loci or non-independent loci. We therefore retained all loci in subsequent analyses.

# Univariate optimization

Landscape variables that were supported by univariate optimization (i.e., that had higher Akaike weight than the null model of isolation by Euclidean distance) differed among regions (Table 3.1). Slope was supported in all three regions, and was the strongest univariate predictor in DEVA and MOJA, as indicated by median  $R^2$ . A Gaussian slope model was preferred over a linear model or break-point model, although the parameters of the Gaussian model (optimal slope, maximum resistance value) differed between regions. Presence of water barriers was associated with increased resistance to gene flow and was the variable with the greatest explanatory power in GRCA, but was not supported in the remaining two regions. Similarly, presence of major roads was associated with increased resistance and was an important variable in MOJA but not in DEVA or GRCA. Distance to water (positively associated with resistance) was supported in DEVA and MOJA, and NDVI (negatively associated with resistance) was supported in DEVA and GRCA, but these variables only explained slightly more variation than Euclidean distance in these regions. Forested areas and anthropogenic development were not supported in any region and were excluded from multivariate optimization. Models with unlogged cost distances were preferred for all variables in all regions, with the exception of the isolation by distance model in GRCA.

# **Multivariate optimization**

The optimized multivariate model for GRCA included slope, water barriers, and distance to water. For MOJA, the optimized multivariate model included slope, roads, and NDVI. The univariate slope model was preferred over all multivariate models for DEVA. Table 3.2 provides details on the relationships between each variable and resistance to gene flow for the optimized multivariate model in each region. Resistance values associated with variables in optimized univariate models sometimes differed from those in optimized multivariate models; for instance, water barriers were assigned a resistance of 1,000 in the best univariate model for GRCA, but a value of 5,000 in the best multivariate model.

Explanatory power of optimized multivariate models was relatively low as measured by model  $R^2$ : cost distances explained less than a quarter of the variation in genetic distances in all regions. The multivariate models for GRCA and MOJA represented only a modest increase in explanatory power over the best univariate model. In the DEVA and MOJA regions, Euclidean distance alone explained at least two thirds as much variation as the best multivariate resistance model. However, distance was a less powerful predictor of genetic differentiation in GRCA, where the barrier effect of the Colorado River explained the majority of variation in genetic distances (Tables 3.1, 3.2). **Simulations** 

# Adaptive allele frequency ( $f_A$ ) was positively associated with selection strength and dispersal threshold in both simulation scenarios. We observed greater increase in $f_A$ in

landscapes with more continuously distributed habitat under both scenarios. Relative differences in  $f_A$  among regions (i.e., the ratio of  $f_A$  for two regions at a given point in time) tended to be larger under the novel allele scenario.

#### Novel allele scenario

Under the novel allele scenario, relatively small increases in  $f_A$  were observed over the simulation period (Fig. 3.2). Even under strong selection,  $f_A$  remained below 0.12 after 100 years. The effect of landscape (i.e., difference in  $f_A$  among regions) was slow to emerge (25-50 years under most conditions) and was more pronounced when selection was stronger and maximum dispersal threshold was larger. GRCA clearly exhibited higher  $f_A$  than DEVA and MOJA for all dispersal thresholds when selection was moderate or strong. Differences in  $f_A$  among DEVA and MOJA were only evident when the high dispersal threshold was used and selection was moderate or strong; for all other combinations of dispersal threshold and selection strength, there was no appreciable difference in  $f_A$  between DEVA and MOJA. Where differences were evident,  $f_A$  tended to be higher for DEVA than for MOJA, consistent with our hypothesis of faster spread of the adaptive allele in regions with more continuously distributed habitat.

#### Pre-existing allele scenario

We observed much greater increases in  $f_A$  over time under the pre-existing allele scenario than the novel allele scenario, with  $f_A$  reaching nearly 0.35 by year 100 under some conditions (Fig. 3.3). For all combinations of selection strength and dispersal threshold that produced differences among regions,  $f_A$  was higher for GRCA than the other regions. When selection was weak to moderate, DEVA and MOJA exhibited similar increases in  $f_A$ . However, when selection was strong, the effect of landscape depended on dispersal threshold: with the low dispersal threshold,  $f_A$  was actually higher in MOJA than DEVA, while  $f_A$  was approximately equal for the two regions with the medium or high dispersal threshold.

#### DISCUSSION

We developed landscape resistance models for desert bighorn sheep in three regions with different habitat configuration and factors affecting resistance to gene flow, and found that these differences among landscapes strongly influenced spread of adaptive genetic variation in subsequent genetic simulations. Observed differences among regions in adaptive allele spread were consistent with expectations of faster spread when landscapes exhibited more continuously distributed habitat and when a pre-existing allele (i.e., standing genetic variation) rather than a novel allele (i.e., mutation) served as the source of adaptive genetic variation. This study is one of the first examples of simulating effects of selection in real-life landscapes for which resistance to gene flow has been empirically estimated, and demonstrates the utility of this approach for making landscape-level inferences about adaptive potential.

#### **Resistance modeling**

Our resistance model optimization suggested that slope and strong dispersal barriers including major water bodies and interstate highways were the dominant landscape factors influencing gene flow for desert bighorn sheep. These results are consistent with previous research demonstrating strong effects of slope and highways on bighorn gene flow in the Mojave Desert (Epps et al. 2005; Epps et al. 2007), but are the first demonstration that major water barriers (i.e., the Colorado River) currently limit gene flow for bighorn sheep. A Gaussian model in which both very low and very high slopes have high resistance was supported, suggesting that some areas of our study regions are actually steep enough to prevent movement by bighorn sheep. Interestingly, the effect of slope appeared to vary by region with respect to the optimal slope and the maximum resistance associated with slope; for instance, slope was assigned a maximum resistance of 100 in DEVA but only 10 in GRCA. It is not clear why sub-optimal slopes would have presented a greater obstacle to bighorn sheep in DEVA than GRCA, but the distribution of favorably sloped terrain within each region may have influenced this result. Habitat in GRCA comprises one highly continuous patch of favorably-sloped terrain (the Grand Canyon), allowing bighorn sheep to travel long distances with limited exposure to highly resistant slopes; in contrast, even short-distance travel between neighboring patches in MOJA typically requires traversing low-slope, high-resistance areas. Thus, the effect of slope may appear to be weaker in GRCA simply because dispersal is minimally limited by slope.

This example illustrates an important and well-known limitation in landscape genetic analyses: features that influence gene flow but are not highly variable within the landscape are often not supported in landscape resistance models (Short Bull et al. 2011). This limitation may also explain why we failed to detect an effect of some landscape variables that are known to strongly influence movement behavior of bighorn sheep (e.g., forested areas, anthropogenic development). The vast majority of each region we examined comprised natural cover types, with anthropogenic development limited to a few peripheral areas, so it may not have been possible to detect an effect of development, even if it strongly influenced dispersal for those few individuals that occupy habitat close to development. Landscape genetic effects are also difficult to detect in highly connected landscapes (Cushman et al. 2013a; Zeller et al. *in review*), where individuals are largely able to avoid traversing through resistant features. This scenario may apply, for instance, to forested areas in the GRCA region, which occur almost exclusively on plateaus surrounding the Grand Canyon – that is, in areas of low slope that are poor bighorn sheep habitat and can be avoided by traveling within the canyon. These examples suggest that spatial extrapolation of locally-developed resistance models could lead to omission of important factors affecting dispersal and gene flow, and researchers wishing to apply resistance models in new areas should recognize this limitation.

Euclidean distance explained at least two thirds as much of the genetic differentiation among individuals as the optimized multivariate model in DEVA and MOJA, suggesting that isolation by distance is strong in these regions. However, distance was a relatively poor predictor of genetic differentiation in GRCA, which was likely driven by the unique juxtaposition of suitable habitat and a major barrier in GRCA: the steeply sloped Grand Canyon provides a long, narrow, and continuous habitat patch for bighorn sheep, but is bisected by the Colorado River running through the bottom of the canyon and serving as a strong barrier to movement. Thus, two individuals on opposite sides of the river that were sampled only hundreds of meters apart may have less chance of mating than two individual on the same side of the river that were sampled tens to hundreds of kilometers apart.

# **Simulating selection**

Genetic simulations revealed differences in the spread of adaptive genetic variation among regions for many combinations of selection strength, dispersal threshold, and scenario. Under moderate to strong selection, we observed higher frequencies of the

adaptive allele in the GRCA region, which had the most continuous distribution of habitat, than in MOJA or DEVA, which had low to intermediate habitat continuity relative to GRCA. Under most combinations of selection strength, dispersal threshold, and scenario that we tested, differences in  $f_A$  that emerged between DEVA and MOJA were also consistent with our hypothesis of faster spread of adaptive alleles in more continuous landscapes; however, because DEVA and MOJA were much more similar with respect to habitat continuity than either was to GRCA, differences between DEVA and MOJA were relatively small. Our results may actually underestimate differences among the regions because population density was assumed to be constant through time and between habitat patches in CDPOP simulations, but densities tend to fluctuate in space and time in real populations. Such fluctuations are likely to be most dramatic in patchy landscapes like the MOJA region that exhibit metapopulation dynamics (Bleich et al. 1996; Schwartz et al. 1986). Theoretical models suggest that extinction and recolonization reduce fixation probability for beneficial alleles (Cherry 2003, 2004), and that probability of fixation of beneficial alleles decreases when reproductive success varies among demes (Whitlock 2003). These effects should be stronger in patchier systems and reinforce the differences we observed between regions.

The effects of selection strength and dispersal threshold on  $f_A$  were generally consistent with our expectations:  $f_A$  increased faster when selection was stronger or dispersal threshold was larger. The effect of dispersal distance on  $f_A$  values was much smaller than the effect of selection in most cases. Our high dispersal threshold was four times larger than our low threshold, but  $f_A$  values tended to be only marginally higher using the high threshold. We suspect that this is because we used an inverse square dispersal function with short-distance movements very common and long-distance movements very rare, such that increasing the maximum dispersal distance may have had only a small influence on the average distance moved by an individual. Exploring dispersal functions was beyond the scope of this study and should be left for future theoretical work.

In some cases, we observed interesting interactions between selection strength and dispersal threshold. The degree to which differences among regions arose during simulations depended on the combination of selection strength and dispersal threshold considered, with regional differences quite pronounced for some combinations and minimal for others. In a few cases, the choice of dispersal threshold even reversed the conclusion regarding the relative spread of adaptive allele in the two relatively patchy regions; for instance, under strong selection in the pre-existing allele scenario,  $f_A$ increased faster for DEVA than MOJA with the medium dispersal threshold, but the opposite was true with the low dispersal threshold. This interplay between dispersal threshold and selection strength is a potentially complex topic that warrants further investigation.

We observed large differences in the trajectory of  $f_A$  under the novel allele and pre-existing allele scenarios. This may be partially due to the fact that initial allele frequencies differed between the scenarios (0.01 versus 0.05), as they were intended to simulate different processes by which adaptive alleles could be introduced and spread throughout a landscape. However, examination of the spatial spread of the adaptive allele under each scenario suggests limitations on inter-patch dispersal imposed by landscape resistance were also likely responsible for the difference between scenarios. As an example, Figure 3.4 shows the spread of the adaptive allele across each region by year 100 under strong selection and moderate dispersal threshold for both scenarios. Under the novel allele scenario, where the adaptive allele was initially present in only one location, spread was limited to nearby patches in DEVA and MOJA, although  $f_A$  within those patches was close to 1. This reflects the presence of high-resistance terrain (e.g., desert flats, possibly with roads) separating patches and making inter-patch dispersal events rare. GRCA, with its highly continuous habitat, exhibited much greater geographic spread, although limited to the side of the Colorado River on which the adaptive allele was initially present. Under the pre-existing allele scenario, however, spread of the adaptive allele was much more extensive in all three regions. This occurred because the adaptive allele was initially present in all patches within each region, and thus increases in  $f_A$  could occur solely through intra-patch dispersal that did not require traversing highresistance terrain. This also explains why regional differences in  $f_A$  were much smaller under the pre-existing allele scenario: habitat patchiness played much less of a limiting role when inter-patch dispersal was not needed to introduce the adaptive allele to new populations.
Given the major differences between the two scenarios, it is helpful to consider the circumstances that could lead to each scenario and the implications of each for adaptation. Novel alleles arise naturally in populations through mutation, but the likelihood of such a mutation giving rise to regional adaptation to climate change or some other stressor is probably low because (1) mutation rates are generally small, so novel alleles should arise infrequently (Allendorf and Luikart 2009), especially in large mammals with long generation times; (2) most mutations are selectively neutral or deleterious (Frankham et al. 2002); and (3) even those mutations that are favored by selection are often lost through genetic drift (Hartl 2007). Therefore, a more likely source of novel alleles is the intentional translocation of one or more individuals from another region that are known to possess favorable traits that could improve survival or reproduction in the target area; for instance, individuals adapted to hotter, drier conditions in a different part of a species' range, or those found to have disease-resistant genotypes, could be translocated. In contrast, the pre-existing allele scenario presupposes that standing genetic variation can provide the source material for adaptation; that is, alleles that exist at low frequency in the population and are maintained by a balance of recurrent mutation, selection, and drift become more favorable as biotic or abiotic environmental conditions change (Barrett and Schluter 2008). Standing genetic variation should lead to faster evolution than is possible with novel mutations, as well as fixation of more alleles with smaller effect and spread of more recessive alleles (Barrett and Schluter 2008); recent case studies (e.g., Steiner et al. 2007) have demonstrated that standing genetic variation can facilitate rapid adaptation to novel conditions. We initialized pre-existing adaptive alleles randomly across each region in our simulations, but it may be more realistic to think of clinal variation associated with an environmental gradient (e.g., temperature or precipitation), or variation that is distributed unevenly across populations due to differences in connectivity or population size.

We explored a very simplistic selection model in which fitness was dependent upon an individual's genotype at a single locus exhibiting additive dominance. However, most quantitative traits are determined by multiple genes (Bürger 2000; Conner and Hartl 2004), and fitness may depend on non-additive effects of alleles at multiple loci (i.e., epistatic effects; Phillips 2008). In addition, we assumed that the adaptive allele in our simulations was universally favored, independent of the environmental characteristics experienced by each individual (i.e., flat selection surfaces). This may be appropriate for some types of adaptive variation (e.g., genes linked with pathogen resistance), but many genes control traits that are directly linked to environmental characteristics (e.g., thermal tolerance limits), and selection will not act in a spatially homogeneous manner if the landscape is heterogeneous with respect to the environmental characteristic of interest. Simulation studies with more realistic selection models will be necessary to fully understand how differences among landscapes contribute to the spatial distribution of adaptive genetic variation. Nevertheless, we have demonstrated an approach that can serve as a starting point for future work incorporating greater ecological and evolutionary complexity and realism.

### Implications for conservation and management

The results of our resistance modeling have important implications for management of connectivity among desert bighorn sheep populations. Beyond the simple distance between individuals, slope and major dispersal barriers (highways and large waterways) were the primary determinants of landscape connectivity. From a conservation perspective, this may be encouraging because the slope of terrain should be negligibly influenced by climate change or anthropogenic development, and barriers to bighorn sheep dispersal can often be mitigated through construction of crossing structures (e.g., Gagnon et al. 2013). NDVI and distance to water were also included in one regional multivariate model and may be more strongly linked to climate change, as forecasted increases in aridity in the southwest U.S. could result in loss of surface water sources and reduction in forage quantity or quality; however, these variables explained a much smaller proportion of the variation in inter-individual genetic distance than did slope and barriers.

Our gene flow simulations suggested that the spread of adaptive genetic variation is likely to occur slowly for desert bighorn sheep, even in places where connectivity has not been compromised and natural selection strongly favors an adaptive allele. In patchy systems like the MOJA region (and to a lesser extent, the DEVA region) where many populations are small, genetic drift can overwhelm selection (Hedrick 2011; Nickerson 2014). The spread of adaptive variation was especially slow for the novel allele scenario, where even an allele that was strongly favored by selection and already present throughout a region at low frequency took 25-50 years to noticeably increase in frequency. Increase in  $f_A$  was considerably faster for the pre-existing allele scenario, but even after 50 years of strong selection,  $f_A$  remained below 0.2 in all regions. Furthermore, this was probably optimistic because we initialized the pre-existing allele scenario assuming that the adaptive allele was already distributed across the entire region and present in all populations, which is unlikely to be true in real-life situations.

The slow pace of selection is partly a reflection of the relatively long generation time of bighorn sheep; the 100-year period of our simulations may seem long from a wildlife conservation and management perspective, but is exceedingly short from an evolutionary perspective, representing fewer than 20 bighorn sheep generations for bighorn sheep. This has two important ramifications. First, relying on existing genetic variation and natural gene flow to promote adaptation to climate change by desert bighorn sheep may not be a realistic conservation option given the rapid forecasted rate of change. Second, if the introduction of novel adaptive alleles to a region via translocation is desired, in may be necessary to target multiple locations within the region to achieve sufficient spread within a time frame relevant to conservation.

## Applications

The framework we have presented here – combining optimization of resistance models and genetic simulations – could be applied by conservationists and managers in a number of ways to help species cope with climate change and other threats to population persistence. It could be used to identify the most effective locations in a region to translocate individuals possessing favorable genotypes with respect to traits such as thermal tolerance or disease resistance, with the goal of maximizing the subsequent spread of adaptive alleles. This approach should not necessarily be limited to large mammals, or even animals; for instance, outplanting resistant tree stock has become a standard practice for restoring forests affected by introduced pests and pathogens (Sniezko 2006), and our approach could potentially improve the efficiency of outplanting programs that can target only a limited number of areas. As our understanding of climatelinked genetic variation improves through advances in population genetics methods and technology (Schoville et al. 2012), so too should our ability to accurately model and predict the spread of adaptive diversity.

### ACKNOWLEDGMENTS

We thank S. Ratchford, W. Sloan, S. Holt, and L. Manning for collecting genetic samples; C. Peterson and M. Corbin for assistance with genotyping; and J. Jaeger and K. Longshore for sharing genetic data for portions of the DEVA region. Funding for this research was provided by the National Park Service's Climate Change Response (PMIS 162673) and Natural Resources Condition Assessment (Cooperative Agreement H8C07080001) programs.

### LITERATURE CITED

- Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64(4):233-247
- Allendorf FW, Luikart G (2009) Conservation and the Genetics of Populations. John Wiley & Sons, Sussex, UK
- Barrett RD, Schluter D (2008) Adaptation from standing genetic variation. Trends in Ecology & Evolution 23(1):38-44
- Berger J (1982) Female breeding age and lamb survival in desert bighorn sheep (*Ovis canadensis*). Mammalia 46(2):183-190
- Bleich VC, Wehausen JD, Ramey II RR, Rechel JL (1996) Metapopulation theory and mountain sheep: implications for conservation. In: McCullough DR (ed), Metapopulations and Wildlife Conservation. Island Press, Covelo, CA
- Bolliger J, Lander T, Balkenhol N (2014) Landscape genetics since 2003: status, challenges and future directions. Landscape Ecology 29(3):361-366
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27(4):325-349
- Bürger R (2000) The mathematical theory of selection, recombination, and mutation. Wiley Chichester, New York
- Castillo JA, Epps CW, Davis AR, Cushman SA (2014) Landscape effects on gene flow for a climate-sensitive montane species, the American pika. Molecular Ecology 23(4):843-856
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333(6045):1024-1026
- Cherry JL (2003) Selection in a subdivided population with local extinction and recolonization. Genetics 164(2):789-795
- Cherry JL (2004) Selection, subdivision and extinction and recolonization. Genetics 166(2):1105-1114

- Conner JK, Hartl DL (2004) A Primer of Ecological Genetics. Sinauer Associates, Sunderland, MA
- Creech TG, Epps CW, Monello RJ, Wehausen JD (2016) Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI. Journal of Arid Environments 127:160-170
- Cushman Samuel A, McKelvey Kevin S, Hayden J, Schwartz Michael K (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. The American Naturalist 168(4):486-499
- Cushman SA, Shirk A, Landguth EL (2012) Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. Landscape Ecology 27(3):369-380
- Cushman SA, Shirk AJ, Landguth EL (2013a) Landscape genetics and limiting factors. Conservation Genetics 14(2):263-274
- Cushman SA, Wasserman TN, Landguth EL, Shirk AJ (2013b) Re-evaluating causal modeling with mantel tests in landscape genetics. Diversity 5(1):51-72
- Diniz-Filho JAF, Soares TN, Lima JS et al (2013) Mantel test in population genetics. Genetics and molecular biology 36(4):475-485
- Dudaniec RY, Rhodes JR, Worthington Wilmer J, Lyons M, Lee KE, McAlpine CA, Carrick FN (2013) Using multilevel models to identify drivers of landscapegenetic structure among management areas. Molecular Ecology 22(14):3752-3765
- Dudaniec RY, Worthington Wilmer J, Hanson JO, Warren M, Bell S, Rhodes JR (2015) Dealing with uncertainty in landscape genetic resistance models: a case of three co-occurring marsupials. Molecular Ecology, doi: 10.1111/mec.13482
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, L. Rechel J (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, McCullough DR (2006) Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15(14):4295-4302
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Frankham R, Ballou JD, Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press, Cambridge
- Gagnon JW, Loberger CD, Sprague SC, Priest M, Boe S, Ogren K, Kombe E, Schweinsburg RE (2013) Evaluation of desert bighorn sheep overpasses along US Highway 93 in Arizona, USA. In: Proceedings of the 2013 International Conference on Ecology and Transportation, Scottsdale, AZ
- Garfin G, Franco G, Blanco H et al (2014) Chapter 20: Southwest. In: Melillo JM, Richmond TC, Yohe GW (eds), Climate Change Impacts in the United States: The Third National Climate Assessment. U.S. Global Climate Change Research Program, Washington, D.C.
- Geist V (1971) Mountain Sheep. Chicago Press, Chicago

- Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22(7):1-19
- Graves TA, Beier P, Royle JA (2013) Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Molecular Ecology 22(15):3888-3903
- Guillot G, Rousset F (2013) Dismantling the Mantel tests. Methods in Ecology and Evolution 4(4):336-344
- Hamel S, Garel M, Festa-Bianchet M, Gaillard J-M, Côté SD (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology 46(3):582-589
- Hartfield M (2012) A framework for estimating the fixation time of an advantageous allele in stepping-stone models. Journal of Evolutionary Biology 25(9):1751-1764
- Hartl DL, Clark AG (2007) Principles of Population Genetics. Sinauer Associates, Sunderland, MA
- Hedrick P (2011) Genetics of Populations. Jones & Bartlett, Sudbury, MA
- Hijmans RJ (2014) raster: Geographic data analysis and modeling. R package version 2.2-31
- Holderegger R, Kamm U, Gugerli F (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. Landscape Ecology 21(6):797-807
- Holderegger R, Wagner HH (2008) Landscape genetics. BioScience 58(3):199-207
- Jaeger JR, Wehausen JD (2012) Development of a habitat management plan to maintain viability of the desert bighorn sheep population in the River Mountains, Nevada: analysis of mitochondrial DNA diversity and connectivity. Final Report to the National Park Service, Lake Mead National Recreation Area. University of Nevada, Las Vegas
- Jones MR, Forester BR, Teufel AI, Adams RV, Anstett DN, Goodrich BA (2013) Integrating landscape genomics and spatially explicit approaches to detect loci under selection in clinal populations. Evolution 67(12):3455-3468
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16(5):1099-1106
- Keyghobadi N, Roland J, Strobeck C (2005) Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity. Molecular Ecology 14(7):1897-1909
- Kierepka EM, Latch EK (2014) Performance of partial statistics in individual-based landscape genetics. Molecular Ecology Resources 15(3):512-525
- Krausman PR, Sandoval AV, Etchberger RC (1999) Natural history of desert bighorn sheep. In: Valdez R, Krausman PR (eds), Mountain Sheep of North America. University of Arizona Press, Tucson
- Landguth E, Cushman S, Schwartz M, McKelvey K, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19(19):4179-4191
- Landguth EL, Cushman SA (2010) CDPOP: A spatially explicit cost distance population genetics program. Molecular Ecology Resources 10(1):156-161

- Landguth EL, Cushman SA, Johnson NA (2012) Simulating natural selection in landscape genetics. Molecular Ecology Resources 12(2):363-368
- Lovich JE, Ennen JR (2011) Wildlife conservation and solar energy development in the desert southwest, United States. BioScience 61(12):982-992
- Manel S, Holderegger R (2013) Ten years of landscape genetics. Trends in Ecology & Evolution 28(10):614-621
- Mehner T, Pohlmann K, Elkin C, Monaghan MT, Freyhof J (2009) Genetic mixing from enhancement stocking in commercially exploited vendace populations. Journal of Applied Ecology 46(6):1340-1349
- Monson G, Sumner L (1980) The Desert Bighorn, Its Life History, Ecology and Management. University of Arizona Press, Tucson
- Nickerson BS (2014) Effects of genetic drift, natural selection, and population connectivity on adaptive-linked genetic diversity of desert bighorn sheep. Master's thesis, Oregon State University, Corvallis
- Oakleaf JR, Kennedy CM, Baruch-Mordo S et al (2015) A world at risk: aggregating development trends to forecast global habitat conversion. PLoS ONE 10(10):e0138334
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637-669
- Phillips PC (2008) Epistasis the essential role of gene interactions in the structure and evolution of genetic systems. Nature Reviews Genetics 9(11):855-867
- Prunier JG, Kaufmann B, Fenet S et al (2013) Optimizing the trade-off between spatial and genetic sampling efforts in patchy populations: towards a better assessment of functional connectivity using an individual-based sampling scheme. Molecular Ecology 22(22):5516-5530
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86(3):248-249
- Rebaudo F, Le Rouzic A, Dupas S, Silvain J-F, Harry M, Dangles O (2013) SimAdapt: an individual-based genetic model for simulating landscape management impacts on populations. Methods in Ecology and Evolution 4(6):595-600
- Rioux Paquette S, Talbot B, Garant D, Mainguy J, Pelletier F (2014) Modelling the dispersal of the two main hosts of the raccoon rabies variant in heterogeneous environments with landscape genetics. Evolutionary Applications 7(7):734-749
- Rubin ES, Boyce WM, Caswell-Chen EP (2002) Modeling demographic processes in an endangered population of bighorn sheep. Journal of Wildlife Management 66(3):796-810
- Schaeffer R, Torres S, Bleich V (2000) Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. California Fish and Game 86(2):127-135
- Schoville SD, Bonin A, François O, Lobreaux S, Melodelima C, Manel S (2012) Adaptive genetic variation on the landscape: methods and cases. Annual Review of Ecology, Evolution, and Systematics 43(1):23-43
- Schwartz MK, Copeland JP, Anderson NJ et al (2009) Wolverine gene flow across a narrow climatic niche. Ecology 90(11):3222-3232

- Schwartz OA, Bleich VC, Holl SA (1986) Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. Biological Conservation 37(2):179-190
- Seager R, Ting M, Li C, Naik N, Cook B, Nakamura J, Liu H (2013) Projections of declining surface-water availability for the southwestern United States. Nature Climate Change 3(5):482-486
- Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19(17):3603-3619
- Shoemaker DD, Jaenike J (1997) Habitat continuity and the genetic structure of Drosophila populations. Evolution 51(4):1326-1332
- Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Molecular Ecology 20(6):1092-1107
- Slatkin M (1976) The rate of spread of an advantageous allele in a subdivided population. In: Karlin S, Nevo E (eds) Population Genetics and Ecology. Academic Press, New York
- Smith SJ, Edmonds J, Hartin CA, Mundra A, Calvin K (2015) Near-term acceleration in the rate of temperature change. Nature Climate Change 5(4):333-336
- Sniezko RA (2006) Resistance breeding against nonnative pathogens in forest trees current successes in North America. Canadian Journal of Plant Pathology 28(S1):S270-S279
- Sork VL, Waits L (2010) Contributions of landscape genetics approaches, insights, and future potential. Molecular Ecology 19(17):3489-3495
- Steiner CC, Weber JN, Hoekstra HE (2007) Adaptive variation in beach mice produced by two interacting pigmentation genes. PLoS Biol 5(9):e219
- U.S. Bureau of Land Management (2015) Soda Mountain Solar Project Final Environmental Impact Statement. Barstow Field Office, Barstow, CA
- Valdez R, Krausman PR (1999) Mountain Sheep of North America. University of Arizona Press, Tucson
- Valière N (2002) GIMLET: a computer program for analysing genetic individual identification data. Molecular ecology notes 2(3):377-379
- van Etten J (2012) gdistance: distances and routes on geographical grids. R package version 1.1-4
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389-395
- Whitlock MC (2003) Fixation probability and time in subdivided populations. Genetics 164(2):767-779
- Wilson L, Blaisdell J, Welsh G, Weaver R, Brigham R, Kelly W, Yoakum J, Hinks M, Turner J, DeForge J (1980) Desert bighorn habitat requirements and management recommendations. Desert Bighorn Council Transactions 24(1):7
- Worthington Wilmer J, Elkin C, Wilcox C, Murray L, Niejalke D, Possingham H (2008) The influence of multiple dispersal mechanisms and landscape structure on population clustering and connectivity in fragmented artesian spring snail populations. Molecular Ecology 17(16):3733-3751

Zeller K, Creech T, Millette K, Crowhurst R, Long R, Wagner H, Balkenhol B, Landguth E (*in review*) Using simulations to evaluate Mantel-based methods for assessing landscape resistance to gene flow. Molecular Ecology

## **TABLES AND FIGURES**

Table 3.1. Optimized univariate resistance models for each region. Variables not included in the table did not outperform the null model of isolation by distance (i.e., had lower median Akaike weight) and were excluded from further analysis.

			Log	
Region	Landscape variable	Optimal resistance surface	transform <sup>1</sup>	Median R <sup>2</sup>
	Slope	Gaussian ( $r_{max}=100, x_{opt}=50, x_{sd}=20$ )	No	0.151
DEVA	Distance to water	Monotonic positive ( $r_{max}=50$ , $r_{exp}=4$ )	No	0.132
	NDVI	Monotonic negative ( $r_{max}=10$ , $r_{exp}=0.25$ )	No	0.130
	Euclidean distance		No	0.129
	Water barriers	Ratio (1,000)	No	0.173
GRCA	Slope	Gaussian ( $r_{max}=10$ , $x_{opt}=50$ , $x_{sd}=20$ )	No	0.062
	Distance to water	Monotonic positive ( $r_{max}=50$ , $r_{exp}=1$ )	No	0.063
	Euclidean distance		Yes	0.050
	Major roads	Ratio (100)	No	0.227
MOJA	Slope	Gaussian ( $r_{max}=10$ , $x_{opt}=40$ , $x_{sd}=20$ )	No	0.200
	NDVI	Monotonic negative ( $r_{max}=100$ , $r_{exp}=0.25$ )	No	0.186
	Euclidean distance		No	0.173

<sup>1</sup> Indicates whether cost distance was log-transformed in resistance model.

Region	Model	Median R <sup>2</sup>
DEVA	<i>slope</i> (Gaussian: r <sub>max</sub> =100, x <sub>opt</sub> =50, x <sub>sd</sub> =20)	0.152
GRCA	water barriers (ratio = 5,000) + slope (Gaussian: $r_{max}=10$ , $x_{opt}=50$ , $x_{sd}=20$ ) + distance to water (positive: $r_{max}=100$ , $r_{exp}=1$ )	0.177
MOJA	roads (ratio = 5,000) + slope (Gaussian: $r_{max}=50$ , $x_{opt}=40$ , $x_{sd}=20$ ) + NDVI (negative: $r_{max}=10$ , $r_{exp}=0.25$ )	0.259

Table 3.2. Optimized multivariate resistance model for each region. For DEVA, the univariate slope model outperformed all multivariate models.



Figure 3.1. Locations where unique genotypes were sampled (black dots) in each of three study regions: A) southern Mojave (n = 378). B) Grand Canyon (n = 252). C) Death Valley (n = 225). Red and blue lines show major barriers to dispersal (highways and waterways, respectively). Hollow black polygons show occupied bighorn habitat within which individuals were randomly located for CDPOP simulations of gene flow.



Figure 3.2. Simulated change in adaptive allele frequency through time under the novel allele scenario for three selection strengths (rows) and three dispersal thresholds (columns) in the DEVA, GRCA, and MOJA regions. Simulations were initiated with a small cluster of adaptive alleles at the center of each region. Solid and dashed lines represent means and 95 percent confidence limits, respectively, from 50 MC replicates per region.



Figure 3.3. Simulated change in adaptive allele frequency through time under the preexisting allele scenario for three selection strengths (rows) and three dispersal thresholds (columns) in the DEVA, GRCA, and MOJA regions. Simulations were initiated with the adaptive allele randomly distributed throughout each region at 5 percent frequency. Solid and dashed lines represent means and 95 percent confidence limits, respectively, from 50 MC replicates per region.



Figure 3.4. Proportion of MC replicates in which adaptive allele is present ( $\geq 1$  copy) in each individual location (represented by a colored dot) at year 100 for each region and each scenario, assuming strong selection and medium dispersal threshold. Black polygons represent national park boundaries.

# CHAPTER 4: GENETIC STRUCTURE AND ADAPTIVE CAPACITY OF DESERT BIGHORN SHEEP IN NATIONAL PARKS OF THE SOUTHWEST UNITED STATES

Tyler G. Creech<sup>1\*</sup>, Clinton W. Epps<sup>1</sup>, John D. Wehausen<sup>2</sup>, Rachel S. Crowhurst<sup>1</sup>, Jef R. Jaeger<sup>3</sup>, Kathleen Longshore<sup>4</sup>, Brandon Holton<sup>5</sup>, William B. Sloan<sup>6</sup>, and Ryan J.

Monello<sup>7</sup>

<sup>1</sup> Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR, USA

<sup>2</sup> White Mountain Research Station, University of California, Bishop, CA, USA

<sup>3</sup> School of Life Sciences, University of Nevada, Las Vegas, NV, USA

<sup>4</sup> Las Vegas Field Station, U.S. Geological Survey, Henderson, NV, USA

<sup>5</sup> Grand Canyon National Park, National Park Service, Grand Canyon, AZ, USA

<sup>6</sup> Southeast Utah Group, National Park Service, Moab, UT, USA

<sup>7</sup> Pacific Island Network, Inventory and Monitoring Program, National Park Service, Hawaii National Park, HI, USA

## ABSTRACT

Climate change presents a major threat to wildlife worldwide, and for many species adaptation will be required to persist in novel environmental conditions. For management agencies tasked with conserving individual species over broad areas, knowledge of how adaptive capacity varies across populations is needed to establish conservation priorities for minimizing climate change impacts. We explored variation in the evolutionary component of adaptive capacity for desert bighorn sheep populations on and near U.S. national parks, comprising a major portion of the subspecies' range. We measured adaptive capacity of populations as a function of two factors that are strongly associated with the potential for evolutionary adaptation: 1) genetic diversity, estimated using neutral microsatellite markers, and 2) connectivity, estimated as the area of occupied habitat within a maximum dispersal range determined using a landscape resistance model. We also used Bayesian clustering and discriminant analysis methods to explore genetic structure across the study area. Populations in Death Valley and Grand Canyon National Parks had the highest genetic diversity and connectivity with surrounding

habitat; consequently, these regions had the greatest adaptive capacity and could serve as genetic refugia from climate change impacts. Populations in eastern Utah and the southern Mojave Desert had the lowest adaptive capacity because of low genetic diversity and/or poor connectivity, and may require conservation actions to improve their potential for adaptation. Genetic structure analyses suggested that populations in eastern Utah are genetically distinct from the rest of the study area, likely resulting from restricted gene flow following regional population extinctions. These results should help guide management of desert bighorn sheep within national parks in the face of climate change.

### **INTRODUCTION**

Climate change is expected to be the greatest threat to biodiversity in many of the world's regions, and could commit up to a third of all species to extinction (Thomas et al. 2004). The vulnerability of species and populations to climate change is strongly influenced by their adaptive capacity - the potential to cope with climate change by persisting *in situ* or moving to more suitable ranges or microhabitats (Dawson et al. 2011). Adaptive capacity is a function of three main components: 1) life-history traits (e.g., dispersal and colonization ability), 2) potential for microevolutionary adaptation via natural selection, and 3) phenotypic plasticity, including behavioral, physiological, or morphological changes (Nicotra et al. 2015; Reed et al. 2011). Assessments of vulnerability to climate change have largely focused on species' ability to track shifts in the spatial distribution of suitable habitat over time (i.e., bioclimatic envelope modeling; Pearson and Dawson 2003). However, *in situ* adaptation could be important for many species (Berteaux et al. 2004; Pulido and Berthold 2004; Skelly et al. 2007; Thomas 2005), particularly species with limited dispersal ability or highly fragmented habitat that prevents range shifts (Schloss et al. 2012) and habitat specialists that may lack suitable habitat under future climate scenarios (Warren et al. 2001).

Of the *in situ* mechanisms for adaptation to climate change, plastic responses may be at least as important as evolutionary responses for many species (Hoffmann and Sgro 2011), although these two mechanisms can be difficult to distinguish (Merilä and Hendry 2014). However, there are limits to plasticity (De Jong 2005; DeWitt et al. 1998; Pigllucci 1996; Valladares et al. 2007) and evolutionary adaptation may provide the only means for persistence in changing environments when these limits are surpassed (Reed et al. 2011). Questions remain about whether species will be able to evolve quickly enough to keep up with the pace of climate change (Hoffmann and Sgro 2011; Skelly et al. 2007), but evidence for evolutionary responses of wildlife populations to rapid climate shifts is accumulating (e.g., Berthold et al. 1992; Karell et al. 2011; Réale et al. 2003).

For management agencies tasked with conserving individual species over broad areas, knowledge of how the potential for evolutionary adaptation varies among populations is needed to establish conservation priorities for minimizing climate change impacts. The spatial distribution of genetic variation among populations, including genetic structure and genetic diversity, can serve as a useful approximation of the adaptive capacity of populations (Hoffmann et al. 2015; Vandergast et al. 2008). Genetic structure analyses can identify populations (or groups of populations) that are genetically distinct and represent unique components of species-level genetic variation, as well as regions where gene flow is restricted and populations are likely to become increasingly genetically isolated. Genetic diversity enables populations to cope with long-term environmental changes, such as climate change (Davis et al. 2005; Hoffmann and Parsons 1997; Stockwell et al. 2003), and is positively associated with fitness (Hansson and Westerberg 2002; Reed and Frankham 2003) and population persistence (Frankham 2005; Lacy 1997; Mills and Smouse 1994). In addition to allowing evolutionary response to climate-related stressors, genetic diversity can lessen the impacts to populations of non-climatic stressors such as disease (Luikart et al. 2008; Spielman et al. 2004).

Connectivity, the degree to which the landscape facilitates movement among populations or habitat patches (Taylor et al. 1993), may also play a key role in evolutionary adaptation to climate change. Connectivity promotes gene flow that results in sharing of genetic variation among populations, and the maintenance of genetic diversity within individual populations (Yamamichi and Innan 2012). There is strong theoretical (Varvio et al. 1986; Wright 1969) and empirical (Epps et al. 2005; Johansson et al. 2007; Young et al. 1996) support for reduced genetic diversity in populations that are isolated by barriers to gene flow. Furthermore, if immigrants to a population originate from areas facing more severe climate stress (e.g., hotter, drier areas), they may be better adapted to climatic stressors and increase the rate of adaptation in that population (Garant et al. 2007; Visser 2008). Connectivity can also indirectly affect genetic diversity and evolutionary potential through its effects on population size and persistence (e.g., Schwalm et al. 2015). Immigration can boost population sizes in declining populations, and in some cases even prevent population extinctions, a process known as demographic rescue (Brown and Kodric-Brown 1977). Larger population size is associated with higher genetic diversity (Frankham 1996) and increased response to selection (Weber 1990) because genetic drift can overwhelm selection in small populations. Individuals in larger populations are also less likely to have reduced fitness due to inbreeding, making them less susceptible to environmental stressors in general (Hedrick 2011; Willi et al. 2006). These and other reasons make improving connectivity one of the most commonly recommended strategies for managing biodiversity in the face of climate change (Heller and Zavaleta 2009).

In this study, we examine the adaptive capacity of desert bighorn sheep (Ovis *canadensis nelsoni*) populations across a major portion of their range by describing their genetic structure, genetic diversity, and connectivity. We focus exclusively on the evolutionary component of adaptive capacity, as opposed to phenotypic plasticity or potential for range shifts, and hereafter use the term "adaptive capacity" in the narrow sense of potential for evolutionary adaptation. Desert bighorn sheep, one of three subspecies of North American bighorn sheep, are culturally and ecologically important ungulates that range across the southwestern U.S. and northern Mexico and are likely to be strongly affected by climate change. They are habitat specialists that rely on steeply sloped terrain with sparse vegetation and good visibility to escape predators (Singer and Gudorf 1999). Throughout much of their range, habitat is discontinuously distributed in small mountain ranges separated by desert flats, although habitat can be relatively continuous in some areas (e.g., Colorado River canyon). Many populations already occupy the highest and wettest potions of their available habitat, so altitudinal migration has limited utility as a climate change adaptation strategy (e.g., Epps et al. 2004). Bighorn sheep possess many of the traits that are associated with high extinction risk and sensitivity to climate change, including low reproductive rate, long life span, slow maturation, poor dispersal ability, and small, isolated populations in many parts of their range (Krausman et al. 1999; Monson and Sumner 1980; Singer and Gudorf 1999).

Individual- and population-level measures of desert bighorn sheep fitness are positively associated with precipitation (Bender and Weisenberger 2005; Douglas 2001; Douglas and Leslie 1986; Epps et al. 2004; Epps et al. 2006; McKinney et al. 2001; Wehausen 2005; Wehausen et al. 1987) and negatively associated with temperature (Douglas 2001; Epps et al. 2004; Epps et al. 2006). Thus, anticipated changes in climate in the desert southwest (e.g., Bachelet et al. 2016) are expected to present a challenge to bighorn populations.

Some of the highest-quality habitat for desert bighorn sheep occurs on lands that are managed by the U.S. National Park Service (NPS) (Epps et al. 2006), which is mandated to conserve wildlife populations "in such a manner and by such means as will leave them unimpaired for the enjoyment of future generations" (U.S. Congress 1916). Bighorn sheep were extirpated from a large portion of their range, including several national parks, by the 1940s, but extensive reintroduction efforts over the past few decades have restored populations in many areas (Singer and Gudorf 1999). Knowledge of genetic structure, genetic diversity, and connectivity of populations on NPS lands is still very limited, however, and is needed to develop strategies for desert bighorn sheep conservation in a rapidly changing climate.

To address this need, we develop an extensive genetic dataset for desert bighorn sheep, including more than 1,600 individuals across 10 national parks and surrounding lands genotyped at neutral microsatellite markers. We use Bayesian clustering and discriminant analysis methods to assess genetic structure across this study area, and calculate genetic diversity metrics for populations. The use of neutral markers as an index of adaptive genetic variation has been questioned, and we address the implication of doing so for this study in the Discussion section. Next, we use a previously developed landscape resistance model (based on analyses in Chapter 3 of this dissertation) to estimate connectivity for each population based on the amount of suitable habitat within a resistance-based dispersal threshold. We then compare adaptive capacity among populations by generating an adaptive capacity score for each population that incorporates the influences of both genetic diversity and connectivity with equal weighting. Although these two factors are expected to be strongly correlated in most natural systems, the relationship between genetic diversity and connectivity is very weak for desert bighorn sheep across our study area as a whole (Appendix N). Numerous translocations during the past 40 years have muddied the relationship between present genetic diversity and landscape connectivity; additionally, contemporary landscape changes (e.g., highway construction) have modified connectivity in some areas, but the genetic effects of these changes have not yet been fully realized (i.e., genetic lag). Thus, we treat these as independent factors, with genetic diversity measuring the current evolutionary potential of populations and connectivity measuring the capacity for populations to maintain that evolutionary potential through gene flow. We use results from the above analyses to identify potential "genetic refugia" - populations whose combination of high genetic diversity and high connectivity makes them most likely to successfully cope with climate change via adaptation (Epps et al. 2006). Finally, we examine how well the existing network of national parks protects adaptive capacity, and discuss the implications of our results for range-wide management of desert bighorn sheep in the face of climate change.

### **METHODS**

### **Study area**

The study area encompassed ten national parks that contain the vast majority of desert bighorn sheep on NPS lands, as well as adjacent lands (e.g., state lands, Bureau of Land Management lands, U.S. Forest Service lands, or Indian reservations) containing population that were likely to interact with those on NPS lands (Fig. 4.1). The study area was heterogeneous with respect to many landscape characteristics that influence bighorn sheep. In all areas, bighorn habitat was defined by steep terrain, which allows bighorn to escape predators, and by proximity to reliable surface water; however, the configuration of such habitat varied considerably across the study area, including areas where habitat was very discretely distributed (e.g., the Mojave Desert metapopulation) and areas where habitat was relatively continuous (e.g., the Grand Canyon area). Three different deserts – the Mojave, Sonoran, and Great Basin deserts – with different climate regimes and biota were represented in the study area (Bender 1982). In most areas the landscape had been minimally altered by anthropogenic development (urbanization, highways, mining, water impoundments, etc.), but the extent of these developments tended to be greater in southern California and Nevada than in the remaining portions of the study area in northern Arizona and southern Utah. The degree to which bighorn sheep population history had been directly influenced by management actions also varied within the study area. Most populations in California and Arizona were extant native populations (Epps et al. 2003), while Utah contained many populations that were reintroduced during the past half century using individuals sourced from distant areas in some cases (Utah Division of Wildlife Resources 2013).

### Genetic sampling and genotyping methods

We used non-invasive sampling of fecal pellets to obtain DNA from individuals across the study area. We combined genetic datasets from multiple projects covering different portions of the study area. Populations in the southern Mojave Desert were sampled between 2000 and 2004 (Epps et al. 2006), populations in southern Nevada and near Lake Mead were sampled between 2003 and 2007 (Jaeger and Wehausen 2012), and a portion of populations in and near Death Valley National Park were sampled between 2003 and 2010. These sampling efforts targeted waterholes where bighorn sheep congregate during the summer months. Populations in all remaining regions of the study area were sampled during 2011-2014, using survey data, radiotelemetry data, and sightings databases from state wildlife agencies and NPS to identify areas in which to focus sampling effort. A small number of blood and tissue samples from live captures, hunter kills, or carcasses discovered in the field were also used as DNA sources.

We compiled or generated genotypes for 1652 individuals at 14-17 neutral microsatellite loci. Samples were processed and genotyped in three different laboratories (corresponding to different projects) using similar techniques. A detailed description of genetic laboratory protocols for the most recent project (samples from 2011-2014) can be found in Appendix I. Details of protocols for earlier sampling periods can be found in Epps et al. (2006) and Jaeger and Wehausen (2012).

### **Defining populations and habitat patches**

We grouped individuals into populations based on the location where they were sampled, then created a habitat patch polygon for each population to use in spatially-explicit analyses (e.g., calculating climate variables associated with populations). In the Mojave and Sonoran deserts, habitat is generally distributed in discrete patches of steeply sloped terrain separated by desert flats; thus, it was relatively straightforward to assign individuals to populations and map these populations' associated habitat patches. We used a ten percent slope cutoff to establish the boundaries of habitat patches in these regions (Epps et al. 2007), and relied on expert opinion to modify boundaries in areas where this cutoff did not accurately represent the extent of habitat known to be used by a population.

In the Great Basin Desert (including the Colorado Plateau), habitat is more continuously distributed and establishing populations and patch boundaries was less straightforward. We defined populations based on the spatial clustering of individuals (i.e., groups of sample locations clearly separately from other groups) and used the genetic clustering program GENELAND (Guillot et al. 2005) to provide additional information on population boundaries when we were unsure whether individuals should be considered part of the same or separate populations. After establishing populations, we created habitat patch polygons by generating a minimum convex polygon (MCP) from sample locations, buffering the MCP by 10 km to reflect that individuals likely used additional areas beyond the MCP, and removing portions of the buffered polygon that were not suitable habitat (e.g., flat areas, water bodies).

This process resulted in a total of 62 populations (and associated habitat patches) across the study area (Fig. 4.1). To allow for broad comparisons across the study area, we grouped populations into six regions based on geographic proximity, similar environments, and administrative boundaries: 1) Southern Mojave, including populations in and around Mojave National Preserve and Joshua Tree National Park; 2) Northern Mojave, including populations in and around Death Valley National Park; 3) Southern Nevada, including populations around the city of Las Vegas and Lake Mead National Recreation Area; 4) Northern Arizona, including populations in Grand Canyon National Park; 5) Southern Utah, including populations in and around Glen Canyon National Recreation Area, Capitol Reef National Park, Grand Staircase-Escalante National Monument, and Zion National Park; and 6) Eastern Utah, including populations in and around Arches National Park, Canyonlands National Park, and the city of Moab.

### **Genetic structure**

We used the Bayesian clustering program STRUCTURE (Pritchard et al. 2000) to describe genetic structure of desert bighorn sheep across the study area. We assumed admixture and correlated allele frequencies among populations, and used the population in which each individual was sampled as a location prior. We included a burn-in of 500,000 steps followed by a run of 500,000 steps to estimate parameters. We checked for convergence in values of summary statistics. The number of clusters (*K*) ranged from 1 to 12, with 10 iterations per *K* value. We determined the most likely number of clusters using the  $\Delta K$  method of Evanno et al. (2005), implemented in STRUCTURE HARVESTER (Earl 2012). We used CLUMPP (Jakobsson and Rosenberg 2007) to estimate average assignment probabilities to each cluster across iterations for each individual. We explored results for all *K* values that exhibited clearly higher  $\Delta K$  than neighboring *K* values to allow for hierarchical population structure. We estimated population-level cluster assignment probabilities by averaging individual assignment probabilities for all individuals in each population at each supported *K* value.

We also evaluated genetic structure using a complementary approach called discriminant analysis of principal components (DAPC), a multivariate method that summarizes between-group genetic differentiation while ignoring within-group variation (Jombart et al. 2010). DAPC makes no assumptions about the underlying population genetic model, and therefore may be a more appropriate clustering method when individuals are distributed not in discrete populations (e.g., the island model of gene flow) but rather continuously across the landscape, resulting in a pattern of isolation by distance (Kalinowski 2011). In addition to detecting genetic clusters, DAPC also describes the relatedness between clusters. We conducted DAPC using the adegenet package (Jombart 2008) for R (R Development Core Team 2014) and used ten replicate runs of K-means clustering to determine the most likely number of genetic clusters. We used alpha-score optimization to determine the number of retained principal components that represented best trade-off between discrimination power and overfitting. We used a scatterplot of the first two discriminant functions to assess cluster relatedness. As with STRUCTURE results, we estimated population-level cluster assignment probabilities by averaging individual assignment probabilities for the most likely number of clusters.

Because initial results suggested a major split between one cluster and all remaining clusters, we repeated the analysis using only the data from these remaining clusters to determine if hierarchical genetic structure could be found.

The presence of missing data in genetic datasets can bias genetic structure results, particularly when missing data is non-randomly distributed across populations or markers. This was true of our dataset because samples from different regions were genotyped in different labs at different sets of microsatellite loci. To address this bias, we ran STRUCTURE and DAPC analyses using a subset of our genetic data that included only ten loci used by all labs and for all geographic regions. We used a database of bighorn sheep translocation records from the Western Association of Fish and Wildlife Agencies (WAFWA) to determine whether populations were native or had a history of translocation (reintroduction or augmentation with individuals from other populations) to aid in interpretation of genetic structure results.

## **Genetic diversity**

We assessed genetic diversity using genotypes at neutral microsatellite loci. For each population we calculated allelic richness  $(A_r)$ , the average number of alleles per locus after correcting for variation in sample sizes among populations, using rarefaction with a minimum sample size of six individuals. To facilitate comparisons with populations from other studies, we also calculated expected heterozygosity  $(H_e)$ , a common genetic diversity metric that does not depend on sample size like  $A_r$  does. However, we used only  $A_r$  values when assessing adaptive capacity, as  $A_r$  is more sensitive than  $H_e$  to population bottlenecks and is considered a better indicator of long-term evolutionary potential (Allendorf and Luikart 2009; Leberg 2002). We used the *gstudio* package (Dyer 2014) for R to calculate both metrics. We used a Mann-Whitney U test to determine whether  $A_r$  differed between populations occupying habitat patches within national parks (defined as having at least 10 percent of habitat patch overlapping park) or and those occupying patches outside of national parks.

## Connectivity

We quantified connectivity of each population as the area of occupied habitat within an estimated maximum dispersal range of its habitat patch, based on a landscape resistance model developed in Chapter 3. Populations surrounded by larger areas of occupied

habitat within their dispersal range should exchange individuals with neighboring populations at higher rates; thus, this definition of connectivity should provide a good indicator of the potential for both gene flow with and demographic rescue by neighboring populations. Occupied habitat area should also serve as a crude indicator of the potential for local movement (i.e., to different microclimates) in response to worsening local conditions. For brevity, we refer to the amount of occupied habitat within dispersal range of a population as "connected habitat" or simply "connectivity," although we acknowledge that the term connectivity has many other interpretations.

We used a resistance-based approach rather than a Euclidean distance-based approach to account for the fact that habitat patches close to each other but separated by terrain that is highly resistant to dispersal (e.g., desert flats or highways) may be less connected than patches that are separated by a long distance but with intervening terrain that is favorable for dispersal. Our resistance model included a Gaussian effect of slope (where moderate slopes were less resistant than low or high slopes) and strong barrier effects of major water bodies and interstate highways (see Appendix M for additional details on resistance model). We used this model to calculate the effective distance (a measure that combines geographic distance and relative habitat resistance) along the least-cost path (Adriaensen et al. 2003) between every pair of individuals within each region. We also calculated the Bray-Curtis distance (a measure of genetic differentiation; Bray and Curtis 1957) between pairs of individuals, and then used Mantel correlograms to identify the effective distance beyond which pairwise genetic distances and effective distances were no longer correlated in each region. We used the mean of these regional estimates as the effective distance threshold for bighorn sheep dispersal. We mapped the area around each population that could be reached by an individual traveling outward from the patch boundary along a least-cost patch until the dispersal threshold was reached (i.e., the effective neighborhood) using ArcGIS 10.0 (ESRI 2010). Finally, we calculated the area of occupied bighorn sheep habitat within the effective neighborhood around each population, using habitat maps created by state wildlife agencies and compiled by WAFWA. We made small modifications to the occupied habitat map in areas where we believed it over- or under-represented habitat (e.g., removal of heavily forested areas that are unlikely to be used by bighorn sheep). We used a Mann-Whitney

U test to determine whether connectivity differed for populations within versus outside of national parks.

### Adaptive capacity

We compared adaptive capacity among populations and regions in two ways. First, we calculated an adaptive capacity score for each population that incorporated the influence of both genetic diversity and population connectivity. We standardized  $A_r$  and connectivity values by subtracting the mean value and dividing by the standard deviation in order to make the two variables comparable. We then averaged these standardized scores to create a single adaptive capacity score. Second, we used a scatterplot of allelic richness versus connectivity of populations to determine the most effective management objectives for each population and region to boost adaptive capacity (i.e., improve genetic diversity and/or connectivity). We identified genetic refugia as those populations that exhibited higher-than-average values of both allelic richness and connectivity. We determined whether habitat patches associated with genetic refugia were protected within a national park or on unprotected lands outside the national parks.

### RESULTS

Table 4.1 contains genetic diversity, connectivity, and adaptive capacity values for each population (or its associated habitat patch). Results for each factor are discussed below. **Genetic structure** 

The likelihood curve from our STRUCTURE analysis increased smoothly with increasing *K* and did not exhibit a clear plateau within the range of *K* values tested (Fig. L.1). Using the Evanno et al. (2005) method to identify the most likely number of clusters, we found the peak value of  $\Delta K$  occurred at K = 2, and a smaller peak suggesting secondary structure occurred at K = 4 (Fig. L.2). Population assignment probabilities for K = 2 indicated a major split between populations to the east of Grand Canyon National Park and those to the west, with populations within Grand Canyon exhibiting strong admixture (Figs. 4.2A, L.3A). Several populations in the S. Utah region (e.g., Zion, Kaiparowits-West) assigned strongly to the western cluster, but this was consistent with translocation history, as individuals sourced from the Lake Mead area were used to augment or reintroduce populations in these areas during the past forty years. Results for

K = 4 indicated that the E. Utah, N. Arizona, and S. Nevada regions each comprised a relatively distinct genetic cluster (Figs. 4.2B, L.3B). The fourth cluster included populations in the N. Mojave and S. Mojave regions, but many of these populations also showed admixture with the S. Nevada cluster. Populations in the S. Utah region showed varying degrees of assignment to the S. Nevada, E. Utah, and N. Arizona clusters, reflecting the long history of translocations from multiple source populations in this region.

Using DAPC, the most likely number of clusters varied from 6 to 13, with a modal value of 10 across the 10 iterations of the clustering algorithm that we ran, suggesting that the program could not reliably determine the number of genetic clusters. However, results from all iterations revealed a single cluster (corresponding to populations in the E. Utah region and parts of the S. Utah region) that was strongly differentiated from all other clusters, with no clear differences between these other clusters (Figs. 4.3A, 4.4A). We removed all of the Utah populations with >10% assignment to this distinct cluster from the dataset and reran the DAPC analysis to see if the clustering algorithm could further resolve genetic structure of the remaining populations after accounting for this primary genetic division within the data. Results suggested that the remaining populations comprised five clusters: relatively distinct clusters corresponding to the N. Arizona and S. Nevada regions, and three less distinct clusters exhibiting overlap primarily between the N. Mojave and S. Mojave regions (Figs. 4.3B, 4.4B).

### **Genetic diversity**

Allelic richness of populations ranged from 2.32 to 3.90 with a mean of 3.24, while expected heterozygosity ranged from 0.44 to 0.70 with a mean of 0.60 (Table 4.1).  $A_r$  and  $H_e$  of populations were highly correlated (Pearson's r = 0.95), and we focus henceforth on  $A_r$  results. The N. Arizona region exhibited the highest genetic diversity of all regions (Figs. 4.5, 4.6). This region included the most genetically diverse population in the study area (Grand Canyon-River Left Mid) and four of the top nine populations. Within N. Arizona, the Grand Canyon-River Left East population had considerably lower  $A_r$  than the other populations, but was still higher than average across the study area. The S. Nevada region had the second highest genetic diversity of the six regions, and very little variation in  $A_r$  among regional populations. The N. Mojave region also had higher-thanaverage genetic diversity, particularly for populations along the east side of Death Valley (e.g., Funeral, Black, and Grapevine Mountains); the White Mountains population stood out as having lower  $A_r$  than the rest of the region. The S. Mojave regions had the greatest variability in  $A_r$  of any region, including some of the least (e.g., San Gabriel Mountains) and most (e.g., Marble Mountains) genetically diverse populations across the study area; on average,  $A_r$  was moderate in this region. Most populations in the S. Utah region had low or moderate genetic diversity, with two exceptions: the Kaiparowits-East and Kaiparowits-West populations were both among the top 12 most genetically diverse populations in the study area. The E. Utah region had consistently low genetic diversity and included the population with the lowest  $A_r$  in the study area (Arches-Gemini Bridges).  $A_r$  was higher (P < 0.001; Fig. 4.5) for populations within national parks (median: 3.38) than for those outside national parks (median: 3.04).

## Connectivity

The area of connected habitat varied from essentially none for the San Gabriel Mountains to over 11,000 km<sup>2</sup> for the S. Panamint population in the N. Mojave region (Table 4.1). Populations in the N. Mojave region had considerably greater connectivity than populations in other regions (Figs. 4.5, 4.6); the ten most connected populations were from this region, and only the White Mountains and Avawatz Mountains populations had more moderate connectivity habitat. Populations in the N. Arizona and E. Utah regions exhibited moderate or greater connectivity, but did not approach the levels observed for most N. Mojave populations. The S. Utah region had moderate connectivity overall, but large variation among populations; for instance, the Zion population had the second smallest area of connected habitat in the study area, but the San Rafael-Dirty Devil population had the 12<sup>th</sup> largest area. Populations in the S. Mojave and S. Nevada regions had lower connectivity than those in other regions (Figs. 4.5, 4.6), which likely reflected the patchy distribution of habitat and presence of major highways and/or water barriers in these regions (Fig. 4.1). Connectivity was greater (P < 0.001; Fig. 4.5) for populations within national parks (median: 3,919 km<sup>2</sup>) than for those outside of national parks (median:  $1,725 \text{ km}^2$ ).

## Adaptive capacity

Adaptive capacity (based on the combination of genetic diversity and connectivity) showed major differences among regions (Fig. 4.5), and among populations within some regions (Table 4.1). Populations in the N. Mojave region had the highest adaptive capacity, closely followed by those in the N. Arizona region (Figs. 4.5, 4.6). The seven highest adaptive capacity scores were from populations in the N. Mojave region, and 14 of the top 16 were from N. Mojave or N. Arizona populations. The S. Nevada and S. Utah regions exhibited moderate adaptive capacity on average, but variation among populations was much greater within the S. Utah region; for instance, the Kaiparowits-West population had the 9<sup>th</sup> highest adaptive capacity, while the Zion populations had the 7<sup>th</sup> lowest. Populations in the S. Mojave and E. Utah regions had the lowest adaptive capacity on average, but variability among populations was considerable in both regions. The Arches-Gemini Bridges population in the E. Utah region had particularly low adaptive capacity, as did several populations at the western edge of the S. Mojave region (e.g., North San Bernardino-Cushenbury Mountains, Newberry/Ord/Rodman Mountains, San Gabriel Mountains). The following populations were identified as genetic refugia based on higher-than-average genetic diversity and connectivity (in descending order of adaptive capacity score): Funeral Mountains, Last Chance Range/Corridor Canyon, S. Panamint Range, Tin Mountain, Cottonwood Canyon, Grapevine Mountains, Black (CA) Mountains, Grand Canyon-River Right East, Kaiparowits-West, Grand Canyon-River Right West, Kaiparowits-East, Henry Mountains, Red Canyon/White Canyon/Scorup Canyon.

### DISCUSSION

We found wide variation among desert bighorn sheep populations and regions with respect to genetic diversity and connectivity, which should ultimately influence the ability of these populations to adapt to climate change (Nicotra et al. 2015). These results are consistent with theoretical and empirical studies indicating that genetic diversity is unevenly distributed among populations of most species (Eckert et al. 2008; Rauch and Bar-Yam 2004), and support the notion that range-wide studies of population genetic diversity are an important component of species-level conservation plans for addressing

climate change impacts. Much emphasis has been placed on identifying and prioritizing species that are most vulnerable to climate change (Foden et al. 2013; Summers et al. 2012; Thomas et al. 2004; Williams et al. 2008); in contrast, our analysis yielded information that will facilitate the prioritization of conservation actions for populations of a single species, an approach that has been employed much less frequently in the context of climate change (e.g., Blair et al. 2012; Davis et al. 2012). We also provide the broadest examination of desert bighorn sheep genetic structure to date, complementing previous studies at the subspecies level (Boyce et al. 1999; Buchalski et al. 2015; Epps et al. *in press;* Gutiérrez-Espeleta et al. 2000) and the species level (Buchalski et al. *in press;* Malaney et al. 2015). We discuss our major findings and their implications for desert bighorn sheep conservation and management below.

### Genetic structure and diversity

Our genetic structure analyses suggested that major genetic divisions are present across the study area and that gene flow has been restricted between some regions. In particular, the E. Utah region appears to be genetically distinct from the remaining regions; both of our clustering methods identified this as the most important genetic split in our study area. The regional history of bighorn sheep populations provides a plausible explanation for this pattern: nearly all populations in southeast Utah went extinct between the late 1800s and the 1940s as a result of habitat conversion, mining impacts, unregulated harvest, and livestock-borne diseases (Singer and Gudorf 1999; Utah Division of Wildlife Resources 2013), leaving only a small remnant population in Canyonlands National Park. This population bottleneck is expected to have reduced genetic diversity of the remnant population and interrupted gene flow with adjacent regions, causing allele frequencies to diverge and making this remnant population increasingly genetically distinct.

Reintroduction of bighorn sheep populations in the E. Utah region beginning in the mid-1970's (Utah Division of Wildlife Resources 2013) likely reinforced this low genetic diversity and genetic isolation because the individuals used to found these populations were sourced from the remnant Canyonlands population. Low genetic diversity of reintroduced desert bighorn sheep populations has been documented in many other studies (e.g., Fitzsimmons et al. 1997; Hedrick et al. 2001; Whittaker et al. 2004), and has often been attributed to founder effects. Although reintroductions appear to have increased gene flow in the E. Utah region, many more generations of gene flow may be required to break down the observed genetic differentiation.

Weaker genetic structure appears to exist in the remainder of the study area. The N. Arizona and S. Nevada regions each comprised a distinct genetic cluster in the DAPC analysis excluding E. Utah populations and in the STRUCURE analysis for K = 4. In contrast, there appears to be little differentiation between the N. Mojave and S. Mojave regions; populations from both regions assigned primarily to the same cluster in STRUCTURE analyses, and DAPC suggested that individuals from these regions were genetically similar. Interstate highways separate these regions and further subdivide the S. Mojave region, and measurable increases in genetic differentiation have already been observed between populations on opposite sides of these highways (Epps et al. 2005); however, these barriers have only existed for 40-70 years, and their full effect on genetic structure may not yet be realized. Further, the interaction of bighorn sheep and interstate highways appears dynamic over time; since 2012, bighorn sheep have been detected crossing Interstate 40 in the S. Mojave in at least one location and genetic data collected during 2013-2015 show that gene flow has been reestablished there (C. Epps, unpublished data).

Genetic diversity was high throughout much of the study area relative to estimates from other parts of the subspecies' range. Populations in the N. Mojave, N. Arizona, and S. Nevada regions are among the most genetically diverse bighorn sheep populations that have been reported in the literature, despite the apparently small and fragmented nature of these populations. Average expected heterozygosity was 0.62 or higher for populations in all three regions, including ten populations with  $H_e > 0.65$ . These estimates are higher than microsatellite-based  $H_e$  estimates for most desert bighorn sheep populations outside our study area: Boyce et al. (1997) reported mean  $H_e$  of 0.549 for populations in the Peninsular Ranges of southern California and 0.498 for populations in southern New Mexico; and Gutierrez-Espeleta et al. (2000) found mean  $H_e$  of 0.57 for populations in southern Arizona.  $H_e$  of populations in our study area also compares favorably to reported estimates for Rocky Mountain bighorn sheep populations, which range from 0.43 – 0.60 (Boyce et al. 1997; Forbes et al. 1995; Gutiérrez-Espeleta et al. 2000). Interpopulation movements likely have played a large role in maintaining this genetic diversity, and thus are extremely important for evolutionary potential.

### Geographic variation in adaptive capacity

Our results suggest that desert bighorn sheep populations vary widely in their capacity to adapt to changing climate, and that some populations could serve as genetic refugia while others will likely require intervention to restore evolutionary potential. Populations in the N. Mojave region, most of which are within Death Valley National Park, had the highest adaptive capacity and comprised the majority of the genetic refugia identified in our analysis. The N. Mojave region had the highest connectivity of any region, which reflects several beneficial characteristics of the landscape in this region: suitable habitat is plentiful in the region; natural barriers to movement between habitat patches are minimal (with the exception of the wide, flat Death Valley); anthropogenic barriers to movement such as major highways, large urban areas, or water impoundments are absent; and other anthropogenic stressors are relatively minimal. Current genetic diversity of N. Mojave populations is very high, and given the strong regional connectivity, is likely to remain high relative to other regions.

N. Arizona populations also scored highly in terms of adaptive capacity because these populations were some of the most genetic diverse in the study area. Despite their exceptional genetic diversity, adaptive capacity of N. Arizona populations was lower than in the N. Mojave region because of limited connectivity. This was an initially surprising result because these populations occupy the Grand Canyon, which is a corridor of nearly continuous habitat extending for several hundred miles. However, this narrow strip of habitat is surrounded by forested plateau that is avoided by bighorn sheep, so the amount of suitable habitat within dispersal range of these populations is limited. This could restrict movement of individuals to new habitat outside of the Grand Canyon, as well as immigration by individuals from other areas.

The S. Utah region had large variation in adaptive capacity among populations resulting from different translocation histories. Populations in the S. Utah region were extirpated by the middle of the 20<sup>th</sup> century like those in the E. Utah region, but some were reintroduced using individuals sourced from genetically diverse populations near Lake Mead rather than (or in addition to) individuals from E. Utah populations. The S.

Utah populations with low adaptive capacity are either poorly connected (e.g., Zion) or were reintroduced using only E. Utah individuals as founders (e.g., Capitol Reef). Populations with high adaptive capacity in this region tended to show ancestry from both S. Nevada and E. Utah clusters and have strong connectivity due to a large amount of surrounding suitable habitat and few dispersal barriers (e.g., Kaiparowits populations).

S. Nevada region populations had moderate adaptive capacity, similar to those in the S. Utah region but with much less variability among populations. Although they had genetic diversity higher than any region except N. Arizona, the S. Nevada populations were among the least connected in the study area because of naturally patchy habitat and the presence of anthropogenic barriers including interstate highways, urban development around Las Vegas, and Lake Mead (Jaeger and Wehausen 2012).

The E. Utah and S. Mojave regions exhibited the lowest adaptive capacity in the study area, but for different reasons: low genetic diversity for the E. Utah region, stemming from population history described above; and poor connectivity for the S. Mojave region as a result of the naturally patchy distribution of habitat and the existence of several interstate highways that have restricted movement between habitat patches (Epps et al. 2005). Populations in both of these regions are possible targets for actions to improve adaptive capacity.

These results underscore the importance of intact, native systems for maintaining the potential for evolutionary adaptation across the range of desert bighorn sheep. Populations in portions of the study area with extant, native populations and few anthropogenic barriers to dispersal, such as those in Death Valley and Grand Canyon National Parks, tended to exhibit relatively high adaptive capacity. In contrast, populations in more fragmented landscapes (e.g., S. Mojave region) or in regions that have been heavily influenced by translocation (e.g., S. and E. Utah regions) tended to have much lower adaptive capacity. This pattern is consistent with previous studies that have found low genetic diversity or fitness in reintroduced bighorn sheep populations (e.g., Whittaker et al. 2004; Wiedmann and Sargeant 2014), and provides further evidence in support of preserving native populations and the landscapes that sustain them.

### Management actions to maximize adaptive capacity

The results of our analysis can be used to guide management of bighorn sheep populations as they are exposed to climate change impacts. For instance, the four quadrants in Figure 4.6 suggest different optimal strategies for maximizing adaptive capacity: increase genetic diversity (upper left quadrant), increase connectivity (lower right), or pursue both goals (lower left). For genetic refugia in the upper right quadrant, the focus should be on maintaining these characteristics.

Translocations of individuals with new genes into genetically depauperate populations have been used to restore genetic diversity and increase fitness for populations of many species, including bighorn sheep (Bouzat et al. 2009; Hedrick 2014; Hogg et al. 2006; Johnson et al. 2010; Miller et al. 2012). More than 2,000 desert bighorn sheep have been translocated since the 1950s, and over half of all current bighorn sheep populations resulted from translocations (Krausman 2000). However, there are risks associated with translocations – most notably, the potential for outbreeding depression and loss of local adaptation when individuals from the source population are adapted to different environmental conditions than individuals in the recipient population (Edmands 2007; Weeks et al. 2011). Long-distance translocation are relatively common in bighorn sheep management (e.g., individuals translocated from the Lake Mead area to the Kaiparowits populations in E. Utah), but the evidence for detrimental effects resulting from such translocations is mixed. Wiedman and Sargeant (2014) found higher recruitment in a population reintroduced using individuals of a similar ecotype to what was originally present at the release site than in a population reintroduced using individuals from different ecotype. However, Whiting et al. (2011) found that reintroduced bighorn sheep from distance source populations were able to adjust the timing and synchrony of parturition to match local conditions within five years of reintroduction, suggesting that adaptation to new environments can occur rapidly for at least some traits. At the very least, caution should be exercised when considering translocations to increase genetic diversity of desert bighorn sheep populations. For populations that are extremely isolated (e.g., Zion) or located in regions with such limited genetic variation that neighboring populations are unlikely to contain new alleles (e.g., E. Utah populations), only long-distance translocation may be possible or useful. A small

number of experimental translocations, with careful monitoring of fitness in the recipient populations over time, would be a prudent first step towards evaluating the costs and benefits of translocations for improving evolutionary potential.

Improving connectivity of bighorn sheep populations presents a substantial challenge. Natural barriers to dispersal – for instance, large expanses of flat terrain between mountain ranges in the southern Mojave Desert - play a large role in restricting gene flow among populations in some areas (Epps et al. 2007). Reductions in connectivity and gene flow due to anthropogenic barriers such as interstate highways can sometimes be addressed with wildlife crossing structures, although costs can be very high (Corlatti et al. 2009). For example, overpasses for desert bighorn sheep have been constructed along Highway 93 the Black Mountains of Arizona and have facilitated > 1,700 crossings in the first three years since their construction (Gagnon et al. 2013). Similar structures in other areas, such as along Interstates 10, 15, and 40 in the S. Mojave region, could greatly enhance regional connectivity (Creech et al. 2014). There may also be opportunities to enhance connectivity by modifying existing infrastructure (e.g., removing highway fencing around underpasses) to encourage bighorn sheep crossings of anthropogenic barriers; in some cases, bighorn sheep may eventually discover routes over or under such barriers (C. Epps, unpublished data). Where connectivity cannot be improved through such modifications to the landscape, periodic translocation of individuals from outside populations could be used to provide gene flow (Weeks et al. 2011).

Our analysis assumed that connectivity benefits desert bighorn sheep populations by enhancing gene flow and thereby helping populations to maintain genetic diversity. However, it must be acknowledged that connectivity can be a double-edged sword: when infectious diseases are present within a landscape, connectivity may promote disease transmission among populations (Hess 1996; Hess 1994; Simberloff and Cox 1987). This threat is particularly acute for bighorn sheep populations, which were decimated by diseases introduced by domestic livestock to many parts of their range beginning with European settlement in the late 1800s (Wehausen et al. 2011). Infectious disease continues to impact desert bighorn populations in our study area today; in the last several years, respiratory disease outbreaks have been detected in numerous populations of the
Mojave Desert metapopulation, as well as many populations in Nevada, Arizona, and Utah (Epps et al. *in preparation;* Roug et al. *in preparation*). Although connectivity is a critical component of adaptive capacity over the long term, the short-term risks of disease transmission should be considered before undertaking management actions to increase dispersal among populations.

Ultimately, any management action that promotes large population sizes should help to preserve genetic diversity because alleles are lost by genetic drift at a faster rate in smaller populations (Hedrick 2011). This could include actions that target climatic or non-climatic stressors, such as maintaining or adding artificial water sources (Dolan 2006; Longshore et al. 2009), controlling predator populations (Ernest et al. 2002; Rominger et al. 2004; Wehausen 1996), enhancing forage quality (e.g., via prescribed burning; Holl et al. 2004), or minimizing disease risk by preventing co-mingling with domestic animals (Wehausen et al. 2011).

#### The role of national parks

Our results highlight the role of the national parks in promoting the adaptive capacity of desert bighorn sheep. Populations occupying habitat at least partially within national parks had higher connectivity and higher genetic diversity on average than populations outside of the national parks, which should enhance their potential for evolutionary adaptation and local movement in response to climate change. All of the populations that we identified as genetic refugia in our analysis occupied habitat patches that were at least partially protected within national parks. This finding is perhaps not surprising, given that national parks were established in some of the most remote parts of the western U.S., where human impacts have been limited over the past two centuries, and their establishment has provided further legal protections against anthropogenic threats (e.g., hunting, mining, grazing highway construction). We expect the contribution of national parks toward protecting high-quality habitat for bighorn sheep to be even more critical going forward as anthropogenic impacts continue to accrue outside the parks (Hansen et al. 2013; Martinuzzi et al. 2015). For instance, the construction of large solar energy facilities in the Mojave Desert may reduce connectivity among bighorn sheep populations in the region (Lovich and Ennen 2011; U.S. Bureau of Land Management United States Dept of Energy 2012).

#### Improving adaptive capacity estimates

We assessed genetic diversity of populations using neutral microsatellite markers because a major goal of this dissertation was to explore landscape influences on gene flow, and neutral markers provide unbiased estimates of demographic processes such as gene flow and genetic drift (Holderegger et al. 2006). Microsatellites are the most widely used markers for inferring genetic diversity and provide important initial estimates of genomewide genetic diversity (Kirk and Freeland 2011); however, evolutionary potential depends on adaptive genetic variation – variation at genes that affect fitness – rather than neutral variation, and the correlation between neutral genetic variation and quantitative variation was found to be weak in a meta-analysis (Reed and Frankham 2001). Our estimates of adaptive capacity could be improved by measuring adaptive genetic variation directly, but genes with adaptive functions linked to climate have not been identified for most non-model organisms, and searching for such genes can be prohibitively expensive and time-consuming (Robledo et al. 2005). Furthermore, there is some evidence to suggest that neutral genetic diversity is a good predictor of adaptive genetic diversity in our study system: Nickerson (2014) found that genetic diversity at neutral and adaptive-linked microsatellite loci were strongly correlated for desert bighorn sheep populations in the Mojave Desert. Thus, we believe our genetic diversity estimates are useful if imperfect indicators of evolutionary potential of bighorn sheep populations in our study area.

Estimates of adaptive capacity could be further refined by incorporating population sizes. To some extent, the effects of population size are already indirectly incorporated into our adaptive capacity estimates because genetic diversity and connectivity are both positively associated with population size. However, incorporating these effects more directly using empirical estimates of population sizes would be preferable. We did not include population size when assessing adaptive capacity because such information is missing for many parts of our study area, and population estimates can also quickly become outdated because population sizes may change dramatically over short time periods due to metapopulation dynamics in some regions (Bleich et al. 1990) or infectious disease outbreaks (Wehausen et al. 2011). Although population surveys are conducted regularly by state agencies, these typically do not extend to adjacent NPS lands where states lack jurisdiction. Better cooperation between state and federal agencies, as well as greater emphasis on thinking beyond administrative boundaries, could make estimates of adaptive capacity more accurate and help to focus conservation effort where it is most needed.

#### From adaptive capacity to climate change vulnerability

We explored one major factor influencing vulnerability of populations to climate change impacts - adaptive capacity - but other factors must be considered when evaluating threats to populations from climate change. In particular, sensitivity (how strongly population dynamics and persistence are linked to climate variables), resilience (the ability to survive and recover from perturbation), and exposure (the rate and magnitude of climate change experienced) contribute to climate change vulnerability (Williams et al. 2008). Sensitivity and resilience are thought to be driven primarily by traits such as reproductive rate, dispersal rate, and physiological tolerance limits (McKinney 1997; Williams et al. 2008) that may vary widely among species but are probably relatively fixed among populations of desert bighorn sheep. However, exposure may vary considerably within in our study area. Climate models predict that mean annual temperature increases will tend to be largest in the northeast portion and smallest in the southwest portion of the study area (Garfin et al. 2014), and that annual precipitation will decline in the southern portion but remain unchanged or increase in the northern portion of the study area (albeit with low confidence; Cayan et al. 2013). A recent study of exposure of U.S. national parks to climate change predicted substantial differences in the magnitude of temperature and precipitation change during this century among parks within our study area (Hansen et al. 2013).

The impact of these temperature and precipitation changes may also depend on how close populations live to their physiological tolerance limits; for instance, a 3 °C temperature increase in the Mojave Desert might be felt more acutely by bighorn sheep in the hotter, drier Iron Mountains than in the cooler, wetter San Gabriel Mountains. This question of whether impacts on populations will be greater in areas experiencing the largest climatic changes or in areas where climatic conditions are closest to tolerance limits has not been well explored (but see Beever et al. 2010). Bioclimatic envelope models that incorporate both the magnitude of climate change and tolerance thresholds could be used to determine which populations are predicted to experience the most dramatic reductions in suitable habitat under future climate scenarios. However, such models would likely need to be developed independently for each region (Schwalm et al. 2015), as the distribution of desert bighorn sheep may be linked with different climatic variables in different parts of the subspecies range.

An additional complicating factor is that indirect effects of climate change through changes in biotic interactions and community composition can also strongly influence population vulnerability (Dawson et al. 2011; Foden et al. 2013; Rapacciuolo et al. 2014; Williams et al. 2008). Indirect effects are likely to vary among bighorn populations within our study area, which is heterogeneous with respect to vegetation, predation pressure, competitor species, and many other ecological characteristics. An assessment of the overall vulnerability of desert bighorn sheep populations to climate change impacts should incorporate all of the above factors to the extent possible; however, the variation in adaptive capacity among populations that we have identified in this analysis should help to guide initial conservation efforts.

#### ACKNOWLEDGMENTS

We thank S. Ratchford, S. Holt, L. Manning, C. Crow, G. Lenhart, M. Miller, J. Spaak, and L. Pilkington for assistance with field logistics and sample collection. C. Peterson and M. Corbin helped with genotyping samples. Funding for this research was provided by a Provost's Distinguished Graduate Fellowship from Oregon State University and the National Park Service's Climate Change Response Program (PMIS 162673).

#### LITERATURE CITED

- Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64(4):233-247
- Allendorf FW, Luikart G (2009) Conservation and the Genetics of Populations. John Wiley & Sons, Sussex, UK
- Bachelet D, Ferschweiler K, Sheehan T, Strittholt J (2016) Climate change effects on southern California deserts. Journal of Arid Environments 127:17-29
- Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1):164-178

- Bender GL (1982) Reference Handbook on the Deserts of North America. Greenwood Press, Westport, Connecticut
- Bender LC, Weisenberger ME (2005) Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico.
   Wildlife Society Bulletin 33(3):956-964
- Berteaux D, Réale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: can arctic life count on evolution? Integrative and Comparative Biology 44(2):140-151
- Berthold P, Helbig A, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. Nature 360(6405):668-670
- Blair ME, Rose RA, Ersts PJ, Sanderson EW, Redford KH, Didier K, Sterling EJ,
  Pearson RG (2012) Incorporating climate change into conservation planning:
  identifying priority areas across a species' range. Frontiers of Biogeography 4(4)
- Bleich VC, Wehausen JD, Holl SA (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4(4):383-390
- Bouzat JL, Johnson JA, Toepfer JE, Simpson SA, Esker TL, Westemeier RL (2009) Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations. Conservation Genetics 10(1):191-201
- Boyce WM, Hedrick PW, Muggli-Cockett NE, Kalinowski S, Penedo M, Ramey-II RR (1997) Genetic variation of major histocompatibility complex and microsatellite loci: a comparison in bighorn sheep. Genetics 145(2):421-433
- Boyce WM, Ramey RR, Rodwell TC, Rubin ES, Singer RS (1999) Population subdivision among desert bighorn sheep (*Ovis canadensis*) ewes revealed by mitochondrial DNA analysis. Molecular Ecology 8(1):99-106
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27(4):325-349
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58(2):445-449
- Buchalski MR, Navarro AY, Boyce WM, Vickers TW, Tobler MW, Nordstrom LA, Garci JA, Gille DA, Penedo MCT, Ryder OA (2015) Genetic population structure of Peninsular bighorn sheep (*Ovis canadensis nelsoni*) indicates substantial gene flow across US–Mexico border. Biological Conservation 184:218-228
- Buchalski MR, Sacks BN, Gille DA, Penedo MCT, Ernest HB, Morrison SA, Boyce WM (*in press*) Phylogeographic and population genetic structure of bighorn sheep (*Ovis canadensis*) in North American deserts. Journal of Mammalogy
- Cayan DR, Tyree M, Kunkel KE, Castro C, Gershunov A, Barsugli J, Ray AJ, Overpeck J, Anderson M, Russell J, Rajagopalan B (2013) Future climate: projected average. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds), Assessment of Climate Change in the Southwest United States. Island Press, Washington, D.C.
- Corlatti L, Hacklaender K, FREY-ROOS F (2009) Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. Conservation Biology 23(3):548-556

- Creech T, Epps C, Monello R, Wehausen J (2014) Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology 29(4):605-619
- Davis AP, Gole TW, Baena S, Moat J (2012) The impact of climate change on indigenous arabica coffee (*Coffea arabica*): predicting future trends and identifying priorities. PLoS ONE 7(11): e47981
- Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. Ecology 86(7):1704-1714
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332(6025):53-58
- De Jong G (2005) Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. New Phytologist 166(1):101-118
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13(2):77-81
- Dolan BF (2006) Water developments and desert bighorn sheep: implications for conservation. Wildlife Society Bulletin 34(3):642-646
- Douglas CL (2001) Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29(1):297-305
- Douglas CL, Leslie DM (1986) Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50(1):153-156
- Dyer RJ (2014) gstudio: Spatial utility functions from the Dyer laboratory. R package version 1.2
- Earl DA (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation genetics resources 4(2):359-361
- Eckert C, Samis K, Lougheed S (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. Molecular Ecology 17(5):1170-1188
- Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology 16(3):463-475
- Epps C, Dekelaita D, Dugovich B (*in preparation*) Updates on respiratory disease affecting desert bighorn sheep in and near Mojave National Preserve.
- Epps CW, Bleich VC, Wehausen JD, Torres SG (2003) Status of bighorn sheep in California. Desert Bighorn Council Transactions 47:20-35
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, L. Rechel J (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, McCullough DR (2006) Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15(14):4295-4302
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038

- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Epps CW, Wehausen JD, Sloan WB et al (*in press*) Fifty years after Welles and Welles: distribution and genetic structure of desert bighorn sheep in Death Valley National Park. Proceedings of the 1st Annual Death Valley Natural History Conference
- Ernest HB, Rubin ES, Boyce WM (2002) Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. Journal of Wildlife Management 66(1):75-85
- ESRI (2010) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14(8):2611-2620
- Fitzsimmons NN, Buskirk SW, Smith MH (1997) Genetic changes in reintroduced Rocky Mountain bighorn sheep populations. Journal of Wildlife Management 61(3):863-872
- Foden WB, Butchart SH, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8(6): e65427
- Forbes SH, Hogg JT, Buchanan FC, Crawford AM, Allendorf FW (1995) Microsatellite evolution in congeneric mammals: domestic and bighorn sheep. Molecular Biology and Evolution 12(6):1106-1113
- Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conservation Biology 10(6):1500-1508
- Frankham R (2005) Genetics and extinction. Biological Conservation 126(2):131-140
- Gagnon JW, Loberger CD, Sprague SC, Priest M, Boe S, Ogren K, Kombe E,
  Schweinsburg RG (2013) Evaluation of desert bighorn sheep overpasses along US
  Highway 93 in Arizona, USA. In: Proceedings of the 2013 International
  Conference on Ecology and Transportation, Scottsdale, AZ
- Garant DANY, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology 21(3):434-443
- Garfin G, Franco G, Blanco H, Comrie A, Gonzalez P, Piechota T, Smyth R, Waskom R (2014) Chapter 20: Southwest. In: Melillo JM, Richmond TC, Yohe GW (eds), Climate Change Impacts in the United States: the Third National Climate Assessment. U.S. Global Climate Change Research Program, Washington, D.C.
- Guillot G, Mortier F, Estoup A (2005) GENELAND: a computer package for landscape genetics. Molecular Ecology Notes 5(3):712-715
- Gutiérrez-Espeleta GA, Kalinowski ST, Boyce WM, Hedrick PW (2000) Genetic variation and population structure in desert bighorn sheep: implications for conservation. Conservation Genetics 1(1):3-15
- Hansen AJ, Piekielek N, Davis C, Haas J, Theobald DM, Gross JE, Monahan WB, Olliff T, Running SW(2013) Exposure of U.S. national parks to land use and climate change 1900–2100. Ecological Applications 24(3):484-502

Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Jordan R, Oakeshott Hansson B, Westerberg L (2002) On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11(12):2467-2474

Hedrick P (2011) Genetics of Populations. Jones & Bartlett, Sudbury, MA

- Hedrick P (2014) Conservation genetics and the persistence and translocation of small populations: bighorn sheep populations as examples. Animal Conservation 17(2):106-114
- Hedrick PW, Gutierrez-Espeleta GA, Lee RN (2001) Founder effect in an island population of bighorn sheep. Molecular Ecology 10(4):851-857
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142(1):14-32
- Hess G (1996) Disease in metapopulation models: implications for conservation. Ecology 77(5):1617-1632
- Hess GR (1994) Conservation corridors and contagious disease: a cautionary note. Conservation Biology 8(1):256-262
- Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Jordan R, Oakeshott J, Weeks A, Joseph L, Lockhart P, Borevitz J, Sgrò C (2015) A framework for incorporating evolutionary genomics into biodiversity conservation and management. Climate Change Responses 2(1):1-24
- Hoffmann AA, Parsons PA (1997) Extreme Environmental Change and Evolution. Cambridge University Press, Cambridge, UK
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470(7335):479-485
- Hogg JT, Forbes SH, Steele BM, Luikart G (2006) Genetic rescue of an insular population of large mammals. Proceedings of the Royal Society B 273(1593):1491-1499
- Holderegger R, Kamm U, Gugerli F (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. Landscape Ecology 21(6):797-807
- Holl SA, Bleich VC, Torres SG (2004) Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967–2002. Wildlife Society Bulletin 32(2):412-426
- Jaeger JR, Wehausen JD (2012) Development of a habitat management plan to maintain viability of the desert bighorn sheep population in the River Mountains, Nevada: analysis of mitochondrial DNA diversity and connectivity. Final Report to the National Park Service, Lake Mead National Recreation Area. University of Nevada, Las Vegas
- Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23(14):1801-1806
- Johansson M, Primmer CR, Merilä J (2007) Does habitat fragmentation reduce fitness and adaptability? A case study of the common frog (*Rana temporaria*). Molecular Ecology 16(13):2693-2700
- Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, Belden RC (2010) Genetic restoration of the Florida panther. Science 329(5999):1641-1645
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24(11):1403-1405

- Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics 11(1):94
- Kalinowski ST (2011) The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. Heredity 106(4):625-632
- Karell P, Ahola K, Karstinen T, Valkama J, Brommer JE (2011) Climate change drives microevolution in a wild bird. Nature Communications 2:208
- Krausman PR (2000) An introduction to the restoration of bighorn sheep. Restoration Ecology 8(4S):3-5
- Krausman PR, Sandoval AV, Etchberger RC (1999) Natural history of desert bighorn sheep. In: Valdez R and Krausman PR (eds), Mountain Sheep of North America. University of Arizona Press, Tucson, AZ
- Lacy RC (1997) Importance of genetic variation to the viability of mammalian populations. Journal of Mammalogy:320-335
- Leberg P (2002) Estimating allelic richness: effects of sample size and bottlenecks. Molecular Ecology 11(11):2445-2449
- Longshore KM, Lowrey C, Thompson DB (2009) Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73(3):280-286
- Lovich JE, Ennen JR (2011) Wildlife conservation and solar energy development in the desert southwest, United States. BioScience 61(12):982-992
- Luikart G, Pilgrim K, Visty J, Ezenwa VO, Schwartz MK (2008) Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. Biology Letters 4(2):228-231
- Malaney JL, Feldman CR, Cox M, Wolff P, Wehausen JD, Matocq MD (2015) Translocated to the fringe: genetic and niche variation in bighorn sheep of the Great Basin and northern Mojave deserts. Diversity and Distributions 21(9):1063-1074
- Martinuzzi S, Radeloff VC, Joppa LN, Hamilton CM, Helmers DP, Plantinga AJ, Lewis DJ (2015) Scenarios of future land use change around United States' protected areas. Biological Conservation 184:446-455
- McKinney ML (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516
- McKinney T, Thornton WS, Hanna JD (2001) Precipitation and desert bighorn sheep in the Mazatzal Mountains, Arizona. Southwestern Naturalist 46(3):345-353
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications 7(1):1-14
- Miller J, Poissant J, Hogg J, Coltman D (2012) Genomic consequences of genetic rescue in an insular population of bighorn sheep (*Ovis canadensis*). Molecular Ecology 21(7):1583-1596
- Mills LS, Smouse PE (1994) Demographic consequences of inbreeding in remnant populations. American Naturalist 144(3):412-431
- Monson G, Sumner L (1980) The Desert Bighorn, Its Life History, Ecology and Management. University of Arizona Press, Tucson

- Nickerson BS (2014) Effects of genetic drift, natural selection, and population connectivity on adaptive-linked genetic diversity of desert bighorn sheep. Master's thesis, Oregon State University, Corvallis
- Nicotra AB, Beever EA, Robertson AL, Hofmann GE, O'Leary J (2015) Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conservation Biology 29(5):1268-1278
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12(5):361-371
- Pigllucci M (1996) How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). Trends in Ecology & Evolution 11(4):168-173
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945-959
- Pulido F, Berthold P (2004) Microevolutionary response to climatic change. Advances in Ecological Research 35:151-183
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rapacciuolo G, Maher SP, Schneider AC, Hammond TT, Jabis MD, Walsh RE, Iknayan KJ, Walden GK, Oldfather MF, Ackerly DD (2014) Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20(9):2841-2855
- Rauch EM, Bar-Yam Y (2004) Theory predicts the uneven distribution of genetic diversity within species. Nature 431(7007):449-452
- Réale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society B 270(1515):591-596
- Reed DH, Frankham R (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. Evolution 55(6):1095-1103
- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17(1):230-237
- Reed TE, Schindler DE, Waples RS (2011) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conservation Biology 25(1):56-63
- Robledo C, Kanninen M, Pedroni L (2005) Tropical forests and adaptation to climate change: in search of synergies. Center for International Forestry Research, Bogor, Indonesia
- Rominger EM, Whitlaw HA, Weybright DL, Dunn WC, Ballard WB (2004) The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68(4):993-999
- Roug A, Gonzales B, Wolff P, Abella R, Torres S, Besser T, Dekelaita D, Powers J, Bleich V, Epps C (in preparation) Respiratory disease in desert bighorn sheep (*Ovis canadensis nelsoni*) of the Mojave desert, California and Nevada
- Schloss CA, Nuñez TA, Lawler JJ (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109(22):8606-8611

- Schwalm D, Epps CW, Rodhouse TJ et al (2015) Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Global Change Biology, doi: 10.1111/gcb.13189
- Simberloff D, Cox J (1987) Consequences and costs of conservation corridors. Conservation Biology 1(1):63-71
- Singer FJ, Gudorf MA (1999) Restoration of bighorn sheep metapopulations in and near 15 national parks: conservation of a severely fragmented species. Volume I: planning, problem definition, key findings, and restoration. U.S. Geological Survey and U.S. Department of the Interior, Open File Report 99-102
- Skelly DK, Joseph LN, Possingham HP, Freidenburg LK, Farrugia TJ, Kinnison MT, Hendry AP (2007) Evolutionary responses to climate change. Conservation Biology 21(5):1353-1355
- Spielman D, Brook B, Briscoe D, Frankham R (2004) Does inbreeding and loss of genetic diversity decrease disease resistance? Conservation Genetics 5(4):439-448
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. Trends in Ecology & Evolution 18(2):94-101
- Summers DM, Bryan BA, Crossman ND, Meyer WS (2012) Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. Global Change Biology 18(7):2335-2348
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68(3):571-573
- Thomas CD (2005) Recent evolutionary effects of climate change. In: Lovejoy TE, Hannah L (eds), Climate Change and Biodiversity, Yale University Press, New Haven, Connecticut
- Thomas CD, Cameron A, Green RE et al (2004) Extinction risk from climate change. Nature 427(6970):145-148
- U.S. Bureau of Land Management, U.S. Department of Energy (2012) Final programmatic environmental impact statement (PEIS) for solar energy development in six southwestern states : executive summary.
- U.S. Congress (1916) The National Park Service Organic Act. 16 U.S.C. 1, 2, 3, and 4.
- Utah Division of Wildlife Resources (2013) Utah bighorn sheep statewide management plan. Utah Department of Natural Resources.
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytologist 176(4):749-763
- Vandergast AG, Bohonak AJ, Hathaway SA, Boys J, Fisher RN (2008) Are hotspots of evolutionary potential adequately protected in southern California? Biological Conservation 141(6):1648-1664
- Varvio S-L, Chakraborty R, Nei M (1986) Genetic variation in subdivided populations and conservation genetics. Heredity 57(2):189-198
- Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B 275(1635):649-659
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414(6859):65-69

- Weber K (1990) Increased selection response in larger populations. I. Selection for wingtip height in *Drosophila melanogaster* at three population sizes. Genetics 125(3):579-584
- Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, Breed MF, James EA, Hoffman AA (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4(6):709-725
- Wehausen J (2005) Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. In: Goerrissen J (ed), Symposium Proceedings for the Sweeney Granite Mountains Desert Research Center 1978–2003; A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, CA
- Wehausen JD (1996) Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24(3):471-479
- Wehausen JD, Bleich VC, Blong B, Russi TL (1987) Recruitment dynamics in a Southern California mountain sheep population. Journal of Wildlife Management 51(1):86-98
- Wehausen JD, Kelley ST, Ramey RR (2011) Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. California Fish and Game 97(1):7-24
- Whiting JC, Bowyer RT, Flinders JT, Eggett DL (2011) Reintroduced bighorn sheep: fitness consequences of adjusting parturition to local environments. Journal of Mammalogy 92(1):213-220
- Whittaker DG, Ostermann SD, Boyce WM, DeWoody (2004) Genetic variability of reintroduced California bighorn sheep in Oregon. Journal of Wildlife Management 68(4):850-859
- Wiedmann BP, Sargeant GA (2014) Ecotypic variation in recruitment of reintroduced bighorn sheep: implications for translocation. Journal of Wildlife Management 78(3):394-401
- Willi Y, van Buskirk J, Hoffmann AA (2006) Limits to the adaptive potential of small populations. Annual Review of Ecology, Evolution, and Systematics 37:433-458
- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 6(12):e325
- Wright S (1969) Evolution and the Genetics of Populations: Vol. 2. The Theory of Gene Frequencies. University of Chicago Press, Chicago, Illinois
- Yamamichi M, Innan H (2012) Estimating the migration rate from genetic variation data. Heredity 108(4):362-363
- Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution 11(10):413-418

# TABLES AND FIGURES

Table 4.1. Characteristics of 62 desert bighorn sheep populations in the study area, including translocation history, proximity to national parks, genetic diversity, connectivity, and adaptive capacity.

Population name	Pop. number <sup>1</sup>	Pop. abbrev. <sup>2</sup>	Sample size <sup>3</sup>	Region	Trans- located <sup>4</sup>	Within park <sup>5</sup>	$H_e^{-6}$	$A_r^7$	Connected habitat (km <sup>2</sup> ) <sup>8</sup>	Adaptive capacity <sup>9</sup>
Arches/Gemini Bridges	1	ARGE	7	E. Utah	Yes	Yes	0.44	2.32	3927.14	-1.15
Avawatz Mtns Black (AZ) Mtns Black (CA) Mtns Cady Mtns Capitol Reef	2 3 4 5 6	AVA BLAZ BLCA CADY CARE	12 38 41 12 25	N. Mojave S. Nevada N. Mojave S. Mojave S. Utah	Yes No No Yes	No Yes Yes No Yes	0.67 0.65 0.61 0.59 0.50	3.41 3.46 3.53 3.15 2.80	2995.41 2144.44 7953.66 730.72 3884.92	0.06 -0.03 1.05 -0.65 -0.55
Castle Peaks/ Castle Mtns/ Piute Range	7	PCC	32	S. Mojave	No	Yes	0.64	3.49	2320.65	0.04
Chemhuevi Mtns Clark Mtns/ S. Spring Range Clipper Mtns	8 9 10	CHE CSS CLIP	7 47 16	S. Mojave S. Mojave S. Mojave	No No No	No Yes No	0.49 0.59 0.65	2.66 3.39 3.21	1534.41 2707.65 983.73	-1.12 -0.02 -0.54
Cottonwood Canyon	11	СОТ	15	N. Mojave	No	Yes	0.64	3.42	10007.81	1.26
Coxcomb Mtns Dodd Spring Eagle Mtns Eldorado Mtns Funeral Mtns Grand Canyon-River Left, East	12 13 14 15 16 17	COX DODD EMO ELD FUN GCRLE	7 8 31 60 69 46	S. Mojave N. Mojave S. Mojave S. Nevada N. Mojave N. Arizona	No No No No No	Yes Yes Yes Yes Yes	0.58 0.63 0.65 0.68 0.69 0.60	3.05 3.12 3.65 3.77 3.87 3.33	2008.66 10317.25 2882.43 2535.66 8245.43 3879.72	-0.56 0.94 0.34 0.42 1.52 0.10
Grand Canyon-River Left, Mid	18	GCRLM	47	N. Arizona	No	Yes	0.69	3.90	3910.62	0.83

	Pop.	Pop.	Sample		Trans-	Within	(	. 7	Connected habitat	Adaptive
Population name	number	abbrev. <sup>2</sup>	size <sup>3</sup>	Region	located <sup>4</sup>	park <sup>3</sup>	$H_e^{o}$	$A_{r'}$	(km <sup>2</sup> ) <sup>8</sup>	capacity <sup>9</sup>
Grand Canyon-River Left, West	19	GCRLW	27	N. Arizona	No	Yes	0.64	3.69	3737.75	0.53
Grand Canyon-River Right, East	20	GCRRE	54	N. Arizona	No	Yes	0.65	3.80	5982.33	1.05
Grand Canyon-River Right, West	21	GCRRW	85	N. Arizona	No	Yes	0.62	3.68	5031.99	0.74
Granite Mtns	22	GRAN	21	S. Mojave	No	Yes	0.63	3.48	1645.12	-0.08
Grapevine Mtns	23	GRAP	25	N. Moiave	No	Yes	0.70	3.79	7282.95	1.26
Henry Mtns	20	HEN	13	S Utah	Ves	Ves	0.64	3.77	55/19.61	0.32
Tiell y Withs	27	TILI	15	5. Otali	105	105	0.04	5.27	5547.01	0.52
Highland Range/ McCullough Range	25	HMC	64	S. Nevada	Yes	No	0.67	3.63	1772.62	0.12
Invo Mtns	26	INYO	31	N Mojave	No	No	0.60	3 21	9631 54	0.94
Iron Bange	20	IRON	11	S Mojave	No	No	0.00	2.53	1846.20	1.23
Kaiparowita East	27	VEAST	22	S. Mojave	No	No	0.40	2.55	1040.29	-1.23
Kalparowits-East	28	KEAS I	22	S. Utan	res	res	0.08	5.05	4077.51	0.34
Kaiparowits-Escalante	29	KESC	15	S. Utah	Yes	Yes	0.63	3.23	6008.91	0.34
Kaiparowits-West	30	KWEST	55	S. Utah	Yes	Yes	0.68	3.90	4737.66	0.97
Kingston Mtns/Mesquite Mtns	31	KME	26	S. Mojave	No	No	0.62	3.40	2963.20	0.04
Island in the Sky	32	ISKY	80	E. Utah	No	Yes	0.47	2.65	5497.23	-0.47
Last Chance Range/Corridor Canyon	33	LACH	22	N. Mojave	Yes	Yes	0.65	3.55	10323.89	1.48
Little San Bernardino Mtns	34	LSB	12	S. Mojave	No	Yes	0.63	3.37	2381.01	-0.09
Marble Mtns	35	MAR	47	S. Mojave	No	No	0.68	3.76	842.66	0.12
Muddy Mtns	36	MUD	34	S Nevada	No	No	0.58	3.18	768 19	-0.61
N. San Barnardino	20		21	Strietada	1.0	1.0	0.00	0.10	, 50.17	5.01
Mtns/Cushonbury	37	NSB	15	S. Mojave	No	No	0.45	2.43	1675.00	-1.38
Willis/Cushelloury			1.5	a			0.44			0.04
N. Spring Range	38	NSP	17	S. Nevada	No	No	0.64	3.38	2546.79	-0.06

Population name	Pop. number <sup>1</sup>	Pop. abbrev. <sup>2</sup>	Sample size <sup>3</sup>	Region	Trans- located <sup>4</sup>	Within park⁵	$H_e^{6}$	$A_r^7$	Connected habitat (km <sup>2</sup> ) <sup>8</sup>	Adaptive capacity <sup>9</sup>
Needles/Lockhart Basin	39	NEED	7	E. Utah	No	Yes	0.57	2.84	7267.45	0.08
Newberry (NV) Mtns	40	NNV	15	S. Nevada	No	Yes	0.68	3.67	1351.54	0.10
Newberry (CA) Mtns/ Ord Mtns/ Rodman Mtns	41	NOR	15	S. Mojave	No	No	0.46	2.43	1676.85	-1.39
Old Dad Peak/ Kelso Mtns/ Marl Mtns/ Indian Spring/ Club Peak	42	ОКМ	37	S. Mojave	No	Yes	0.52	3.01	2122.20	-0.59
Old Woman Mtns Orocopia Mtns	43 44	OWO ORO	26 18	S. Mojave S. Mojave	No No	No No	0.51 0.57	2.95 2.91	1914.77 2127.61	-0.70 -0.72
Palen Mtns/Riverside Granite Mtns	45	PRG	10	S. Mojave	No	No	0.61	2.92	1024.22	-0.89
Panamint Buttes Professor Valley Providence Mtns Queen Mtn Red Canyon/ White	46 47 48 49	PANB PROF PROV QUE	12 13 20 11	N. Mojave E. Utah S. Mojave S. Mojave	No Yes No No	Yes No Yes Yes	0.55 0.57 0.63 0.59	3.00 2.76 3.38 3.18	10585.50 4430.11 1874.63 2580.80	0.84 -0.51 -0.17 -0.30
Canyon/ Scorup Canyon River Mtns S. Bristol Mtns	50 51 52	SCOR RVNV SBR	14 46 14	S. Utah S. Nevada S. Mojave	Yes No No	Yes Yes No	0.64 0.64 0.60	3.26 3.48 3.18	4805.71 2569.97 761.92	0.18 0.07 -0.61
S. Panamint Range San Gabriel Mtns	53 54	SPAN SGA	29 6	N. Mojave S. Mojave	No No	Yes No	0.60 0.51	3.31 2.49	11108.43 1.22	1.32 -1.60
San Gorgonio Mtns	55	SGO	17	S. Mojave	No	No	0.54	2.70	2351.21	-0.94
San Juan River	56	SJRV	30	S. Utah	Yes	Yes	0.64	3.19	3465.90	-0.14
San Kafael-Dirty Devil River	57	SRDD	11	S. Utah	Yes	Yes	0.61	3.08	6725.31	0.28

									Connected	
	Pop.	Pop.	Sample		Trans-	Within			habitat	Adaptive
Population name	number <sup>1</sup>	abbrev. <sup>2</sup>	size <sup>3</sup>	Region	located <sup>4</sup>	park <sup>5</sup>	$H_e^{-6}$	$A_r^7$	$(km^2)^8$	capacity9
Tin Mtn	58	TIN	22	N. Mojave	No	Yes	0.65	3.58	8891.49	1.27
Turtle Mtns	59	TUR	14	S. Mojave	No	No	0.59	3.18	1680.61	-0.46
White Mtns	60	WHT	25	N. Mojave	Yes	No	0.52	2.74	5233.49	-0.39
Wood Mtns/ Hackberry Mtns	61	WHA	23	S. Mojave	No	Yes	0.61	3.34	1904.73	-0.22
Zion	62	ZION	21	S. Utah	Yes	Yes	0.55	2.94	549.58	-0.95

<sup>1</sup> Population number used in Figure 4.1

<sup>2</sup> Population abbreviation used in Figure 4.6
 <sup>3</sup> Number of unique genotypes (i.e., individuals) sampled in population

<sup>4</sup> Indicates whether population has received individuals translocated from outside populations

<sup>5</sup> Indicates whether population's habitat patch is at least partially within ( $\geq 10$  % overlap) a national park

<sup>6</sup> Allelic richness, a measure of population genetic diversity

<sup>7</sup> Expected heterozygosity, a measure of population genetic diversity

<sup>8</sup> Area of occupied habitat within a maximum dispersal distance determined by landscape resistance model

<sup>9</sup> Score indicating adaptive capacity as a function of a population's genetic diversity and connectivity (equally weighted); zero represents mean adaptive capacity across all 62 study populations, with higher values indicating higher adaptive capacity



Figure 4.1. Map of study area including ten national parks (colored polygons) and 62 desert bighorn sheep populations (numbered hollow gray polygons) included in analysis. Major water barriers and interstate highways are shown in dark blue and red, respectively. Population names and abbreviations are enumerated in Table 4.1.



Figure 4.2. Cluster assignment probabilities from STRUCTURE analysis for 62 desert bighorn sheep populations. A) Results for K=2. B) Results for K=4. Major water barriers and interstate highways are shown in dark blue and red, respectively. Light green polygons show national parks. Tan polygons show habitat patches associated with populations. Partial assignments at cluster edges (e.g., blue or red cluster assignments for populations in the southwest corner of the study area) likely reflect influence from other clusters outside the study area, rather than affinity to that particular cluster.



Figure 4.3. Scatterplots of first two principal component axes from DAPC analyses for 62 desert bighorn sheep populations. Dots represent individuals, colors and corresponding numbers represent inferred clusters, and ellipses represent 95 percent confidence regions for clusters. Clusters that are farther apart and have less overlap in the scatterplot are more genetically distinct. A) Results of initial analysis including all populations in study area. Orange cluster (#7, Utah) corresponds to orange color in Figure 4.4A, with remaining clusters colored gray in Figure 4.4A. B) Results of secondary analysis including populations not assigned to distinct Utah cluster (#7 in panel A). Cluster colors correspond to colors in Figure 4.4B, and show distinction between the California (N. and S. Mojave), S. Nevada, and N. Arizona populations of bighorn sheep.



Figure 4.4. Population assignments to clusters from DAPC analysis for 62 desert bighorn sheep populations. A) Results of initial analysis including all populations in study area. B) Results of secondary analysis including populations not assigned to distinct Utah cluster (labeled cluster 7 in Fig. 4.3A). Major water barriers and interstate highways are shown in dark blue and red, respectively. Light green polygons show national parks. Tan polygons show habitat patches associated with populations.



Figure 4.5. Comparison of genetic diversity, connectivity, and adaptive capacity across regions (left panels) and between populations within versus outside national parks (right panel). Genetic diversity is measured as allelic richness. Connectivity is measured as the area of occupied habitat within dispersal range of a population. Adaptive capacity score combines genetic diversity and connectivity with equal weights; zero represents the mean adaptive capacity across 62 populations in this study. Boxes show interquartile ranges and horizontal bars show medians. Whiskers extend to the most extreme values that are no more than 1.5 times the interquartile range above or below the box. Outliers are shown as points.



Figure 4.6. Adaptive capacity of 62 desert bighorn sheep populations as a function of genetic diversity (measured as allelic richness) and connectivity (measured as the amount of occupied habitat within dispersal range of a population). Dashed lines represent mean values of each variable across populations. Each population is represented by a single point that is color coded by region. For full population names, refer to Table 4.1.

### GENERAL CONCLUSION

The threats facing desert bighorn sheep are substantial. Climate models predict a hotter and potentially drier environment for the southwest U.S. in coming decades (Cayan et al. 2013), which could place stress on populations that may already be living close to their physiological tolerance limits. Substantial increases in human impacts are predicted in some parts of the desert bighorn sheep's range (Hansen et al. 2013). In the Mojave Desert, for instance, utility-scale solar energy development is ongoing and may compromise metapopulation connectivity if dispersal corridors are disturbed (Lovich and Ennen 2011; U.S. Bureau of Land Management 2015). On top of this, more acute stressors like recent respiratory disease outbreaks in the southern Mojave Desert (Roug et al. in preparation) have affected and will continue to affect populations. Landscape-level conservation tools are needed to help desert bighorn sheep cope with these challenges.

The results of this research should help to guide management of desert bighorn sheep as changes to the landscapes they inhabit continue to accrue. Chapter 1 identified potential opportunities to improve connectivity in the Mojave Desert metapopulation through the restoration of dispersal corridors and populations in empty habitat patches; that analysis suggested that dramatic increases in regional connectivity are possible with a small number of actions, such as constructing crossing structures across three interstate highways that currently fragment the Mojave metapopulation. Chapter 2 validated NDVI as a tool for studying spatial and temporal variation in diet quality of bighorn sheep, and the applications of this tool are manifold. For instance, NDVI could be used to determine which habitat patches have the most favorable forage conditions and should be highest priority for reintroductions, addition of artificial water sources, or land use protections. Chapter 3 provided a comparison across regions of the landscape variables influencing gene flow, and illustrated the effects of regional differences on the spread of adaptive genetic variation. That analysis revealed that adaptive alleles are likely to spread much faster through regions with relatively continuous habitat (e.g., the Grand Canyon) than those with discrete habitat (e.g., the Mojave metapopulation) – information that will help to focus attention on areas where adaptive responses to environmental change are likely to be slow and may require intervention. Chapter 4 explored genetic diversity and

connectivity of populations to determine their capacity for adaptation to climate change. I identified genetically diverse, well-connected populations that could serve as genetic refugia, as well as populations with poor adaptive capacity that may require conservation actions such as genetic restoration or connectivity improvements in order to successfully cope with climate change impacts.

The approaches presented in this dissertation can also be applied to conservation and management of other wildlife species. Network theory has broad applications for studying connectivity in metapopulations or other fragmented systems (Galpern et al. 2011; Urban et al. 2009), and in combination with landscape resistance models can serve as a rigorous method for identifying and prioritizing possible actions to maximize landscape-level connectivity. NDVI and other remotely-sensed vegetation indices have great promise for expanding the scope of diet quality monitoring of wildlife species (Pettorelli et al. 2011), provided that assumptions like those examined in Chapter 2 are met. Simulations of gene flow across empirically-derived landscape resistance surfaces can help wildlife managers predict the effects of landscape changes on the genetic diversity and genetic structure of wildlife populations (Epperson et al. 2010); if natural selection is incorporated, simulations can also predict landscape effects on adaptive genetic variation that influences evolutionary potential of populations (Landguth et al. 2012). Range-wide studies of genetic structure and diversity are fundamental to understanding how adaptive capacity currently varies among populations (Hoffmann et al. 2015), and estimates of functional connectivity of populations based on landscape resistance models can provide addition insights into how well populations will maintain genetic diversity and adaptive capacity over time. These and other landscape genetic approaches can be powerful tools for anticipating and mitigating impacts to wildlife populations from climate change and human land use.

#### LITERATURE CITED

Cayan DR, Tyree M, Kunkel KE, Castro C, Gershunov A, Barsugli J, Ray AJ, Overpeck J, Anderson M, Russell J, Rajagopalan B (2013) Future climate: projected average. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds), Assessment of Climate Change in the Southwest United States. Island Press, Washington, D.C.

- Epperson BK, McRae BH, Scribner KIM, Cusham SA, Rosenberg MS, Fortin M-J, James PMA, Murphy M, Manel S, Legendre P, Dale MRT (2010) Utility of computer simulations in landscape genetics. Molecular Ecology 19(17):3549-3564
- Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. Biological Conservation 144(1):44-55
- Hansen AJ, Piekielek N, Davis C, Haas J, Theobald DM, Gross JE, Monahan WB, Olliff T, Running SW(2013) Exposure of U.S. national parks to land use and climate change 1900–2100. Ecological Applications 24(3):484-502
- Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Jordan R, Oakeshott J, Weeks A, Joseph L, Lockhart P, Borevitz J, Sgrò C (2015) A framework for incorporating evolutionary genomics into biodiversity conservation and management. Climate Change Responses 2(1):1-24
- Landguth EL, Cushman SA, Johnson NA (2012) Simulating natural selection in landscape genetics. Molecular Ecology Resources 12(2):363-368
- Lovich JE, Ennen JR (2011) Wildlife conservation and solar energy development in the desert southwest, United States. BioScience 61(12):982-992
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, Kausrud K (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46(1):15-27
- Roug A, Gonzales B, Wolff P, Abella R, Torres S, Besser T, Dekelaita D, Powers J, Bleich V, Epps C (in preparation) Respiratory disease in desert bighorn sheep (*Ovis canadensis nelsoni*) of the Mojave desert, California and Nevada
- U.S. Bureau of Land Management (2015) Soda Mountain Solar Project Final Environmental Impact Statement. Barstow Field Office, Barstow, CA
- Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. Ecology Letters 12(3):260-273

## BIBLIOGRAPHY

- Adriaensen F, Chardon JP, De Blust G, Swinnen E, Villalba S, Gulinck H, Matthysen E (2003) The application of 'least-cost' modelling as a functional landscape model. Landscape and Urban Planning 64(4):233-247
- Albert EM, Fortuna MA, Godoy JA, Bascompte J (2013) Assessing the robustness of networks of spatial genetic variation. Ecology Letters 16:86-93
- Albon S, Langvatn R (1992) Plant phenology and the benefits of migration in a temperate ungulate. Oikos 65( 3):502-513
- Allendorf FW, Luikart G (2009) Conservation and the Genetics of Populations. John Wiley & Sons, Sussex, UK
- Bachelet D, Ferschweiler K, Sheehan T, Strittholt J (2016) Climate change effects on southern California deserts. Journal of Arid Environments 127:17-29
- Barrett RD, Schluter D (2008) Adaptation from standing genetic variation. Trends in Ecology & Evolution 23(1):38-44
- Beatley JC (1974) Phenological events and their environmental triggers in Mojave Desert ecosystems. Ecology 55(4):856-863
- Beever EA, Ray C, Mote PW, Wilkening JL (2010) Testing alternative models of climate-mediated extirpations. Ecological Applications 20(1):164-178
- Bender GL (1982) Reference Handbook on the Deserts of North America. Greenwood Press, Westport, Connecticut
- Bender LC, Weisenberger ME (2005) Precipitation, density, and population dynamics of desert bighorn sheep on San Andres National Wildlife Refuge, New Mexico. Wildlife Society Bulletin 33(3):956-964
- Bennett AF (1999) Linkages in the Landscape: The Role of Corridors and Connectivity in Wildlife Conservation. IUCN, Gland, Switzerland and Cambridge, UK
- Berger J (1982) Female breeding age and lamb survival in desert bighorn sheep (*Ovis canadensis*). Mammalia 46(2):183-190
- Bernstein L, Pachauri RK, Reisinger A, Intergovernmental Panel on Climate Change (2008) Climate change 2007: synthesis report. IPCC, Geneva, Switzerland
- Berteaux D, Réale D, McAdam AG, Boutin S (2004) Keeping pace with fast climate change: can arctic life count on evolution? Integrative and Comparative Biology 44(2):140-151
- Berthold P, Helbig A, Mohr G, Querner U (1992) Rapid microevolution of migratory behaviour in a wild bird species. Nature 360(6405):668-670
- Bissonette JA (2012) Wildlife and Landscape Ecology: Effects of Pattern and Scale. Springer Science+Business Media, New York
- Blair ME, Rose RA, Ersts PJ, Sanderson EW, Redford KH, Didier K, Sterling EJ,
  Pearson RG (2012) Incorporating climate change into conservation planning:
  identifying priority areas across a species' range. Frontiers of Biogeography 4(4)
- Blanchard P, Festa-Bianchet M, Gaillard J-M, Jorgenson JT (2003) A test of long-term fecal nitrogen monitoring to evaluate nutritional status in bighorn sheep. The Journal of Wildlife Management 67(3):477-484

- Bleich VC, Wehausen JD, Holl SA (1990) Desert-dwelling mountain sheep: conservation implications of a naturally fragmented distribution. Conservation Biology 4(4):383-390
- Bleich VC, Wehausen JD, Ramey II RR, Rechel JL (1996) Metapopulation theory and mountain sheep: implications for conservation. In: McCullough DR (ed), Metapopulations and Wildlife Conservation. Island Press, Covelo, CA
- Bolliger J, Lander T, Balkenhol N (2014) Landscape genetics since 2003: status, challenges and future directions. Landscape Ecology 29(3):361-366
- Boone RB, Thirgood SJ, Hopcraft JGC (2006) Serengeti wildebeest migratory patterns modeled from rainfall and new vegetation growth. Ecology 87(8):1987-1994
- Bouzat JL, Johnson JA, Toepfer JE, Simpson SA, Esker TL, Westemeier RL (2009) Beyond the beneficial effects of translocations as an effective tool for the genetic restoration of isolated populations. Conservation Genetics 10(1):191-201
- Boyce WM, Hedrick PW, Muggli-Cockett NE, Kalinowski S, Penedo M, Ramey-II RR (1997) Genetic variation of major histocompatibility complex and microsatellite loci: a comparison in bighorn sheep. Genetics 145(2):421-433
- Boyce WM, Ramey RR, Rodwell TC, Rubin ES, Singer RS (1999) Population subdivision among desert bighorn sheep (*Ovis canadensis*) ewes revealed by mitochondrial DNA analysis. Molecular Ecology 8(1):99-106
- Bray JR, Curtis JT (1957) An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27(4):325-349
- Brown JH, Kodric-Brown A (1977) Turnover rates in insular biogeography: effect of immigration on extinction. Ecology 58(2):445-449
- Buchalski MR, Navarro AY, Boyce WM, Vickers TW, Tobler MW, Nordstrom LA, Garci JA, Gille DA, Penedo MCT, Ryder OA (2015) Genetic population structure of Peninsular bighorn sheep (*Ovis canadensis nelsoni*) indicates substantial gene flow across US–Mexico border. Biological Conservation 184:218-228
- Buchalski MR, Sacks BN, Gille DA, Penedo MCT, Ernest HB, Morrison SA, Boyce WM (*in press*) Phylogeographic and population genetic structure of bighorn sheep (*Ovis canadensis*) in North American deserts. Journal of Mammalogy
- Buchanan FC, Crawford AM (1992a) Ovine dinucleotide repeat polymorphism at the MAF209 locus. Animal Genetics 23(2):183
- Buchanan FC, Crawford AM (1992b) Ovine dinucleotide repeat polymorphism at the MAF33 locus. Animal Genetics 23(2):186.
- Buchanan FC, Crawford AM (1993) Ovine microsatellites at the OarFCB11, OarFCB128, OarFCB193, OarFCB266, and OarFCB304 loci. Animal Genetics 24(2):145.
- Buchanan FC, Swarbrick PA, Crawford AM (1991) Ovine dinucleotide repeat polymorphism at the MAF65 locus. Animal Genetics 23(S1):85
- Buchanan FC, Swarbrick PA, Crawford AM (1992) Ovine dinucleotide repeat polymorphism at the MAF48 locus. Animal Genetics 22(4):379-380
- Bürger R (2000) The mathematical theory of selection, recombination, and mutation. Wiley Chichester, New York
- Castillo JA, Epps CW, Davis AR, Cushman SA (2014) Landscape effects on gene flow for a climate-sensitive montane species, the American pika. Molecular Ecology 23(4):843-856

- Cayan DR, Tyree M, Kunkel KE, Castro C, Gershunov A, Barsugli J, Ray AJ, Overpeck J, Anderson M, Russell J, Rajagopalan B (2013) Future climate: projected average. In: Garfin G, Jardine A, Merideth R, Black M, LeRoy S (eds), Assessment of Climate Change in the Southwest United States. Island Press, Washington, D.C.
- Chardon J, Adriaensen F, Matthysen E (2003) Incorporating landscape elements into a connectivity measure: a case study for the speckled wood butterfly (*Pararge aegeria* L.). Landscape Ecology 18(6):561-573
- Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD (2011) Rapid range shifts of species associated with high levels of climate warming. Science 333(6045):1024-1026
- Cherry JL (2003) Selection in a subdivided population with local extinction and recolonization. Genetics 164(2):789-795
- Cherry JL (2004) Selection, subdivision and extinction and recolonization. Genetics 166(2):1105-1114
- Chetkiewicz C-LB, Boyce MS (2009) Use of resource selection functions to identify conservation corridors. Journal of Applied Ecology 46(5):1036-1047
- Conner JK, Hartl DL (2004) A Primer of Ecological Genetics. Sinauer Associates, Sunderland, MA
- Corlatti L, Hacklaender K, FREY-ROOS F (2009) Ability of wildlife overpasses to provide connectivity and prevent genetic isolation. Conservation Biology 23(3):548-556
- Crawford AM, Dodds KG, Ede AJ, Pierson CA, Montgomery GW, Garmonsway HG, Beattie AE, Davies K, Maddox JF, Kappes SW, Stone RT, Nguyen TC, Penty FM, Lord EA, Broom JA, Buitkamp J, Schwaiger W, Epplen JT, Matthew P, Matthews ME, Hulme DJ, Beh KJ, McGraw RA, Beattie CW (1995) An autosomal genetic linkage map of the sheep genome. Genetics 140(2):703-724
- Creech T, Epps C, Monello R, Wehausen J (2014) Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology 29(4):605-619
- Creech TG, Epps CW, Monello RJ, Wehausen JD (2016) Predicting diet quality and genetic diversity of a desert-adapted ungulate with NDVI. Journal of Arid Environments 127:160-170
- Crooks KR, Sanjayan MA (2006) Connectivity Conservation. Cambridge University Press, Cambridge
- Crow JF, Kimura M (1970) An Introduction to Population Genetics Theory. Harper and Row, New York.
- Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal, Complex Systems 1695:38
- Cushman SA, Chase M, Griffin C (2010) Mapping landscape resistance to identify corridors and barriers for elephant movement in southern Africa. In: Cushman SA, Huettman F (eds), Spatial Complexity, Informatics, and Wildlife Conservation. Springer, Tokyo
- Cushman SA, McKelvey KS, Hayden J, Schwartz MK (2006) Gene flow in complex landscapes: testing multiple hypotheses with causal modeling. The American Naturalist 168(4):486-499

- Cushman SA, Shirk A, Landguth EL (2012) Separating the effects of habitat area, fragmentation and matrix resistance on genetic differentiation in complex landscapes. Landscape Ecology 27(3):369-380
- Cushman SA, Shirk AJ, Landguth EL (2013a) Landscape genetics and limiting factors. Conservation Genetics 14(2):263-274
- Cushman SA, Wasserman TN, Landguth EL, Shirk AJ (2013b) Re-evaluating causal modeling with mantel tests in landscape genetics. Diversity 5(1):51-72
- Dall'Olmo G, Karnieli A (2002) Monitoring phenological cycles of desert ecosystems using NDVI and LST data derived from NOAA-AVHRR imagery. International Journal of Remote Sensing 23(19):4055-4071
- Davis AP, Gole TW, Baena S, Moat J (2012) The impact of climate change on indigenous arabica coffee (*Coffea arabica*): predicting future trends and identifying priorities. PLoS ONE 7(11): e47981
- Davis MB, Shaw RG, Etterson JR (2005) Evolutionary responses to changing climate. Ecology 86(7):1704-1714
- Dawson TP, Jackson ST, House JI, Prentice IC, Mace GM (2011) Beyond predictions: biodiversity conservation in a changing climate. Science 332(6025):53-58
- De Jong G (2005) Evolution of phenotypic plasticity: patterns of plasticity and the emergence of ecotypes. New Phytologist 166(1):101-118
- De La Maza M, Lima M, Meserve PL, Gutierrez JR, Jaksic FM (2009) Primary production dynamics and climate variability: ecological consequences in semiarid Chile. Global Change Biology 15(5):1116-1126
- DeWitt TJ, Sih A, Wilson DS (1998) Costs and limits of phenotypic plasticity. Trends in Ecology & Evolution 13(2):77-81
- Dijkstra EW (1959) A note on two problems in connexion with graphs. Numerische Mathematik 1(1):269-271
- Diniz-Filho JAF, Soares TN, Lima JS et al (2013) Mantel test in population genetics. Genetics and molecular biology 36(4):475-485
- Dolan BF (2006) Water developments and desert bighorn sheep: implications for conservation. Wildlife Society Bulletin 34(3):642-646
- Douglas CL (2001) Weather, disease, and bighorn lamb survival during 23 years in Canyonlands National Park. Wildlife Society Bulletin 29(1):297-305
- Douglas CL, Leslie DM (1986) Influence of weather and density on lamb survival of desert mountain sheep. Journal of Wildlife Management 50(1):153-156
- Dudaniec RY, Rhodes JR, Worthington Wilmer J, Lyons M, Lee KE, McAlpine CA, Carrick FN (2013) Using multilevel models to identify drivers of landscapegenetic structure among management areas. Molecular Ecology 22(14):3752-3765
- Dudaniec RY, Worthington Wilmer J, Hanson JO, Warren M, Bell S, Rhodes JR (2015) Dealing with uncertainty in landscape genetic resistance models: a case of three co-occurring marsupials. Molecular Ecology, doi: 10.1111/mec.13482
- Dyer RJ (2014) gstudio: Spatial utility functions from the Dyer laboratory. R package version 1.2
- Dyer RJ, Nason JD (2004) Population Graphs: the graph theoretic shape of genetic structure. Molecular Ecology 13(7):1713-1727

- Earl DA (2012) STRUCTURE HARVESTER: a website and program for visualizing STRUCTURE output and implementing the Evanno method. Conservation genetics resources 4(2):359-361
- Eckert C, Samis K, Lougheed S (2008) Genetic variation across species' geographical ranges: the central–marginal hypothesis and beyond. Molecular Ecology 17(5):1170-1188
- Ede AJ, Pierson CA, Henry H, Crawford AM (1994) Ovine microsatellites at the OarAE64, OarHH22, OarHH56, OarHH62, and OarVH4 loci. Animal Genetics 25(1):51-52
- Ede AJ, Pierson CA, Crawford AM (1995) Ovine microsatellites at the OarCP9, OarCP16, OarCP20, OarCP21, OarCP23, and OarCP26 loci. Animal Genetics 26(2):129-130
- Edmands S (2007) Between a rock and a hard place: evaluating the relative risks of inbreeding and outbreeding for conservation and management. Molecular Ecology 16(3):463-475
- Epperson BK, McRae BH, Scribner KIM, Cusham SA, Rosenberg MS, Fortin M-J, James PMA, Murphy M, Manel S, Legendre P, Dale MRT (2010) Utility of computer simulations in landscape genetics. Molecular Ecology 19(17):3549-3564
- Epps C, Dekelaita D, Dugovich B (*in preparation*) Updates on respiratory disease affecting desert bighorn sheep in and near Mojave National Preserve.
- Epps CW, Bleich VC, Wehausen JD, Torres SG (2003) Status of bighorn sheep in California. Desert Bighorn Council Transactions 47:20-35
- Epps CW, McCullough DR, Wehausen JD, Bleich VC, L. Rechel J (2004) Effects of climate change on population persistence of desert-dwelling mountain sheep in California. Conservation Biology 18(1):102-113
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, McCullough DR (2006) Elevation and connectivity define genetic refugia for mountain sheep as climate warms. Molecular Ecology 15(14):4295-4302
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wasser SK, Keim JL, Mutayoba BM, Brashares JS (2013) Quantifying past and present connectivity illuminates a rapidly changing landscape for the African elephant. Molecular Ecology
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Epps CW, Wehausen JD, Palsbøll PJ, McCullough DR (2010) Using genetic tools to track desert bighorn sheep colonizations. Journal of Wildlife Management 74(3):522-531
- Epps CW, Wehausen JD, Sloan WB et al (*in press*) Fifty years after Welles and Welles: distribution and genetic structure of desert bighorn sheep in Death Valley National Park. Proceedings of the 1st Annual Death Valley Natural History Conference

- Ernest HB, Rubin ES, Boyce WM (2002) Fecal DNA analysis and risk assessment of mountain lion predation of bighorn sheep. Journal of Wildlife Management 66(1):75-85
- ESRI (2010) ArcGIS Desktop: Release 10. Environmental Systems Research Institute, Redlands, CA
- Evanno G, Regnaut S, Goudet J (2005) Detecting the number of clusters of individuals using the software STRUCTURE: a simulation study. Molecular Ecology 14(8):2611-2620
- Festa-Bianchet M (1988) Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75(4):580-586
- Fitzsimmons NN, Buskirk SW, Smith MH (1997) Genetic changes in reintroduced Rocky Mountain bighorn sheep populations. Journal of Wildlife Management 61(3):863-872
- Foden WB, Butchart SH, Stuart SN, Vié J-C, Akçakaya HR, Angulo A, DeVantier LM, Gutsche A, Turak E, Cao L (2013) Identifying the world's most climate change vulnerable species: a systematic trait-based assessment of all birds, amphibians and corals. PLoS ONE 8(6): e65427
- Forbes SH, Hogg JT, Buchanan FC, Crawford AM, Allendorf FW (1995) Microsatellite evolution in congeneric mammals: domestic and bighorn sheep. Molecular Biology and Evolution 12(6):1106-1113
- Fortuna MA, Gómez-Rodríguez C, Bascompte J (2006) Spatial network structure and amphibian persistence in stochastic environments. Proceedings of the Royal Society B: Biological Sciences 273(1592):1429-1434
- Frankham R (1996) Relationship of genetic variation to population size in wildlife. Conservation Biology 10(6):1500-1508
- Frankham R (2005) Genetics and extinction. Biological Conservation 126(2):131-140
- Frankham R, Ballou JD, Briscoe DA (2002) Introduction to Conservation Genetics. Cambridge University Press, Cambridge
- Galpern P, Manseau M, Fall A (2011) Patch-based graphs of landscape connectivity: a guide to construction, analysis and application for conservation. Biological Conservation 144(1):44-55
- Gao F, Morisette JT, Wolfe RE, Ederer G, Pedelty J, Masuoka E, Myneni R, Tan B, Nightingale J (2008) An algorithm to produce temporally and spatially continuous MODIS-LAI time series. Geoscience and Remote Sensing Letters, IEEE 5(1):60-64
- Gagnon JW, Loberger CD, Sprague SC, Priest M, Boe S, Ogren K, Kombe E, Schweinsburg RE (2013) Evaluation of desert bighorn sheep overpasses along US Highway 93 in Arizona, USA. In: Proceedings of the 2013 International Conference on Ecology and Transportation, Scottsdale, AZ
- Garant DANY, Forde SE, Hendry AP (2007) The multifarious effects of dispersal and gene flow on contemporary adaptation. Functional Ecology 21(3):434-443
- Garfin G, Franco G, Blanco H, Comrie A, Gonzalez P, Piechota T, Smyth R, Waskom R (2014) Chapter 20: Southwest. In: Melillo JM, Richmond TC, Yohe GW (eds), Climate Change Impacts in the United States: the Third National Climate Assessment. U.S. Global Climate Change Research Program, Washington, D.C.

- Garroway CJ, Bowman J, Carr D, Wilson PJ (2008) Applications of graph theory to landscape genetics. Evolutionary Applications 1(4):620-630
- Geist V (1971) Mountain Sheep. Chicago Press, Chicago
- Georges M, Massey J (1992) Polymorphic DNA markers in Bovidae. In: WO Publication No. 92/13120. World Intellectual Property Organisation, Geneva
- Goslee SC, Urban DL (2007) The ecodist package for dissimilarity-based analysis of ecological data. Journal of Statistical Software 22(7):1-19
- Goudet J (2001) FSTAT, version 2.9.3, A program to estimate and test gene diversities and fixation indices. Lausanne University, Lausanne, Switzerland
- Graves TA, Beier P, Royle JA (2013) Current approaches using genetic distances produce poor estimates of landscape resistance to interindividual dispersal. Molecular Ecology 22(15):3888-3903
- Guillot G, Mortier F, Estoup A (2005) GENELAND: a computer package for landscape genetics. Molecular Ecology Notes 5(3):712-715
- Guillot G, Rousset F (2013) Dismantling the Mantel tests. Methods in Ecology and Evolution 4(4):336-344
- Gustafson EJ, Gardner RH (1996) The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77(1):94-107
- Gutiérrez-Espeleta GA, Kalinowski ST, Boyce WM, Hedrick PW (2000) Genetic variation and population structure in desert bighorn sheep: implications for conservation. Conservation Genetics 1(1):3-15
- Hamel S, Garel M, Festa-Bianchet M, Gaillard J-M, Côté SD (2009) Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. Journal of Applied Ecology46(3):582-589
- Hansen AJ, Piekielek N, Davis C, Haas J, Theobald DM, Gross JE, Monahan WB, Olliff T, Running SW(2013) Exposure of U.S. national parks to land use and climate change 1900–2100. Ecological Applications 24(3):484-502
- Hanski I (1994) A practical model of metapopulation dynamics. Journal of Animal Ecology 63(1):151-162
- Hartfield M (2012) A framework for estimating the fixation time of an advantageous allele in stepping-stone models. Journal of Evolutionary Biology 25(9):1751-1764
- Hartl DL, Clark AG (2007) Principles of Population Genetics. Sinauer Associates, Sunderland, MA
- Hedrick P (2011) Genetics of Populations. Jones & Bartlett, Sudbury, MA
- Hedrick P (2014) Conservation genetics and the persistence and translocation of small populations: bighorn sheep populations as examples. Animal Conservation 17(2):106-114
- Hedrick PW, Gutierrez-Espeleta GA, Lee RN (2001) Founder effect in an island population of bighorn sheep. Molecular Ecology 10(4):851-857
- Heller NE, Zavaleta ES (2009) Biodiversity management in the face of climate change: a review of 22 years of recommendations. Biological Conservation 142(1):14-32
- Helrich K (1990) Official Methods of Analysis of the Association of Official Analytical Chemists. The Association, Arlington, VA

- Henry HM, Penty JM, Pierson CA, Crawford AM (1993) Ovine microsatellites at the OarHH35, OarHH41, OarHH44, OarHH47 and OarHH64 loci. Animal Genetics 24(3):222
- Herfindal I, Solberg E, Sæther B-E, Høgda K, Andersen R (2006) Environmental phenology and geographical gradients in moose body mass. Oecologia 150(2):213-224
- Hess G (1996) Disease in metapopulation models: implications for conservation. Ecology 77(5):1617-1632
- Hess GR (1994) Conservation corridors and contagious disease: a cautionary note. Conservation Biology 8(1):256-262
- Hijmans RJ (2014) raster: Geographic data analysis and modeling. R package version 2.2-31
- Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Jordan R, Oakeshott J, Hansson B, Westerberg L (2002) On the correlation between heterozygosity and fitness in natural populations. Molecular Ecology 11(12):2467-2474
- Hoffmann A, Griffin P, Dillon S, Catullo R, Rane R, Jordan R, Oakeshott J, Weeks A, Joseph L, Lockhart P, Borevitz J, Sgrò C (2015) A framework for incorporating evolutionary genomics into biodiversity conservation and management. Climate Change Responses 2(1):1-24
- Hoffmann AA, Parsons PA (1997) Extreme Environmental Change and Evolution. Cambridge University Press, Cambridge, UK
- Hoffmann AA, Sgro CM (2011) Climate change and evolutionary adaptation. Nature 470(7335):479-485
- Hogg JT, Forbes SH, Steele BM, Luikart G (2006) Genetic rescue of an insular population of large mammals. Proceedings of the Royal Society B 273(1593):1491-1499
- Holderegger R, Kamm U, Gugerli F (2006) Adaptive vs. neutral genetic diversity: implications for landscape genetics. Landscape Ecology 21(6):797-807
- Holderegger R, Wagner HH (2008) Landscape genetics. BioScience 58(3):199-207
- Holl SA, Bleich VC, Torres SG (2004) Population dynamics of bighorn sheep in the San Gabriel Mountains, California, 1967–2002. Wildlife Society Bulletin 32(2):412-426
- Holsinger KE, Weir BS (2009) Genetics in geographically structured populations: defining, estimating and interpreting F<sub>ST</sub>. Nature Reviews Genetics 10(9):639-650
- Horwitz W (1965) Official Methods of Analysis of the Association of Official Agricultural Chemists. The Association, Washington, DC
- Hoyle M, James M (2005) Global warming, human population pressure, and viability of the world's smallest butterfly. Conservation Biology 19(4):1113-1124
- Huete A, Tucker C (1991) Investigation of soil influences in AVHRR red and nearinfrared vegetation index imagery. International Journal of Remote Sensing 12(6):1223-1242
- Irwin LL, Cook JG, McWhirter DE, Smith SG, Arnett EB (1993) Assessing winter dietary quality in bighorn sheep via fecal nitrogen. Journal of Wildlife Management 57(2):413-421

- Jakobsson M, Rosenberg NA (2007) CLUMPP: a cluster matching and permutation program for dealing with label switching and multimodality in analysis of population structure. Bioinformatics 23(14):1801-1806
- Jaeger JR, Wehausen JD (2012) Development of a habitat management plan to maintain viability of the desert bighorn sheep population in the River Mountains, Nevada: analysis of mitochondrial DNA diversity and connectivity. Final Report to the National Park Service, Lake Mead National Recreation Area. University of Nevada, Las Vegas
- Jenks JA, Leslie Jr DM, Lochmiller RL, Melchiors MA, Warde WD (1989) Effect of compositing samples on analysis of fecal nitrogen. Journal of Wildlife Management 53(1):213-215
- Johansson M, Primmer CR, Merilä J (2007) Does habitat fragmentation reduce fitness and adaptability? A case study of the common frog (*Rana temporaria*). Molecular Ecology 16(13):2693-2700
- Johnson WE, Onorato DP, Roelke ME, Land ED, Cunningham M, Belden RC (2010) Genetic restoration of the Florida panther. Science 329(5999):1641-1645
- Jombart T (2008) adegenet: a R package for the multivariate analysis of genetic markers. Bioinformatics 24(11):1403-1405
- Jombart T, Devillard S, Balloux F (2010) Discriminant analysis of principal components: a new method for the analysis of genetically structured populations. BMC Genetics 11(1):94
- Jones MR, Forester BR, Teufel AI, Adams RV, Anstett DN, Goodrich BA (2013) Integrating landscape genomics and spatially explicit approaches to detect loci under selection in clinal populations. Evolution 67(12):3455-3468
- Jordán F, Báldi A, Orci KM, Rácz I, Varga Z (2003) Characterizing the importance of habitat patches and corridors in maintaining the landscape connectivity of a *Pholidoptera transsylvanica* (Orthoptera) metapopulation. Landscape Ecology 18(1):83-92
- Kalinowski ST (2011) The computer program STRUCTURE does not reliably identify the main genetic clusters within species: simulations and implications for human population structure. Heredity 106(4):625-632
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program cervus accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16(5):1099-1106
- Karell P, Ahola K, Karstinen T, Valkama J, Brommer JE (2011) Climate change drives microevolution in a wild bird. Nature Communications 2:208
- Kaufman YJ, Tanre D (1992) Atmospherically resistant vegetation index (ARVI) for EOS-MODIS. Geoscience and Remote Sensing, IEEE Transactions on 30(2):261-270
- Keller D, Holderegger R, van Strien M, Bolliger J (2015) How to make landscape genetics beneficial for conservation management? Conservation Genetics 16(3):503-512
- Keyghobadi N, Roland J, Strobeck C (2005) Genetic differentiation and gene flow among populations of the alpine butterfly, *Parnassius smintheus*, vary with landscape connectivity. Molecular Ecology 14(7):1897-1909

- Kierepka EM, Latch EK (2014) Performance of partial statistics in individual-based landscape genetics. Molecular Ecology Resources 15(3):512-525
- Krausman PR (2000) An introduction to the restoration of bighorn sheep. Restoration Ecology 8(4S):3-5
- Krausman PR, Sandoval AV, Etchberger RC (1999) Natural history of desert bighorn sheep. In: Valdez R and Krausman PR (eds), Mountain Sheep of North America. University of Arizona Press, Tucson, AZ
- Krausman PR, Wehausen JD, Wallace MC, Etchberger RC (1993) Rumen characteristics of desert races of mountain sheep and desert mule deer. The Southwestern Naturalist 38( 2):172-174
- Lacy RC (1997) Importance of genetic variation to the viability of mammalian populations. Journal of Mammalogy:320-335
- Laita A, Kotiaho J, Mönkkönen M (2011) Graph-theoretic connectivity measures: what do they tell us about connectivity? Landscape Ecology 26(7):951-967
- Landguth E, Cushman S, Schwartz M, McKelvey K, Murphy M, Luikart G (2010) Quantifying the lag time to detect barriers in landscape genetics. Molecular Ecology 19(19):4179-4191
- Landguth EL, Cushman SA (2010) CDPOP: A spatially explicit cost distance population genetics program. Molecular Ecology Resources 10(1):156-161
- Landguth EL, Cushman SA, Johnson NA (2012) Simulating natural selection in landscape genetics. Molecular Ecology Resources 12(2):363-368
- Leberg P (2002) Estimating allelic richness: effects of sample size and bottlenecks. Molecular Ecology 11(11):2445-2449
- Lendrum PE, Anderson CR, Monteith KL, Jenks JA, Bowyer RT (2014) Relating the movement of a rapidly migrating ungulate to spatiotemporal patterns of forage quality. Mammalian Biology-Zeitschrift für Säugetierkunde 79(6):369-375
- Leslie DM, Bowyer RT, Jenks JA (2008) Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. Journal of Wildlife Management 72(6):1420-1433
- Leslie DM, Douglas CL (1980) Human disturbance at water sources of desert bighorn sheep. Wildlife Society Bulletin 8(4):284-290
- Levins R (1969) Some demographic and genetic consequences of environmental heterogeneity for biological control. Bulletin of the ESA 15(3):237-240
- Longshore KM, Lowrey C, Thompson DB (2009) Compensating for diminishing natural water: predicting the impacts of water development on summer habitat of desert bighorn sheep. Journal of Arid Environments 73(3):280-286
- Lookingbill TR, Gardner RH, Ferrari JR, Keller CE (2010) Combining a dispersal model with network theory to assess habitat connectivity. Ecological Applications 20(2):427-441
- Lovich JE, Ennen JR (2011) Wildlife conservation and solar energy development in the desert southwest, United States. BioScience 61(12):982-992
- Luikart G, Pilgrim K, Visty J, Ezenwa VO, Schwartz MK (2008) Candidate gene microsatellite variation is associated with parasitism in wild bighorn sheep. Biology Letters 4(2):228-231
- Malaney JL, Feldman CR, Cox M, Wolff P, Wehausen JD, Matocq MD (2015) Translocated to the fringe: genetic and niche variation in bighorn sheep of the

Great Basin and northern Mojave deserts. Diversity and Distributions 21(9):1063-1074

- Manel S, Holderegger R (2013) Ten years of landscape genetics. Trends in Ecology & Evolution 28(10):614-621
- Manel S, Schwartz MK, Luikart G, Taberlet P (2003) Landscape genetics: combining landscape ecology and population genetics. Trends in Ecology & Evolution 18(4):189-197
- Martinez-Jauregui M, San Miguel-Ayanz A, Mysterud A, Rodriguez-Vigal C, Clutton-Brock T, Langvatn R, Coulson T (2009) Are local weather, NDVI and NAO consistent determinants of red deer weight across three contrasting European countries? Global Change Biology 15(7):1727-1738
- Martinuzzi S, Radeloff VC, Joppa LN, Hamilton CM, Helmers DP, Plantinga AJ, Lewis DJ (2015) Scenarios of future land use change around United States' protected areas. Biological Conservation 184:446-455
- McKinney ML (1997) Extinction vulnerability and selectivity: combining ecological and paleontological views. Annual Review of Ecology and Systematics 28:495-516
- McKinney T, Thornton WS, Hanna JD (2001) Precipitation and desert bighorn sheep in the Mazatzal Mountains, Arizona. Southwestern Naturalist 46(3):345-353
- McNaughton SJ (1990) Mineral nutrition and seasonal movements of African migratory ungulates. Nature 345(6276):613-615
- McRae BH, Beier P (2007) Circuit theory predicts gene flow in plant and animal populations. Proceedings of the National Academy of Sciences 104(50):19885-19890
- McRae BH, Dickson BG, Keitt TH, Shah VB (2008) Using circuit theory to model connectivity in ecology, evolution, and conservation. Ecology 89(10):2712-2724
- McRae BH, Hall SA, Beier P, Theobald DM (2012) Where to restore ecological connectivity? Detecting barriers and quantifying restoration benefits. PLoS ONE 7(12):e52604
- Mehner T, Pohlmann K, Elkin C, Monaghan MT, Freyhof J (2009) Genetic mixing from enhancement stocking in commercially exploited vendace populations. Journal of Applied Ecology 46(6):1340-1349
- Merilä J, Hendry AP (2014) Climate change, adaptation, and phenotypic plasticity: the problem and the evidence. Evolutionary Applications 7(1):1-14
- Miller J, Poissant J, Hogg J, Coltman D (2012) Genomic consequences of genetic rescue in an insular population of bighorn sheep (*Ovis canadensis*). Molecular Ecology 21(7):1583-1596
- Mills L (2007) Conservation of wildlife populations: demography, genetics, and management. Blackwell Publishing, Malden, MA
- Mills LS, Smouse PE (1994) Demographic consequences of inbreeding in remnant populations. American Naturalist 144(3):412-431
- Minor ES, Urban DL (2007) Graph theory as a proxy for spatially explicit population models in conservation planning. Ecological Applications 17(6):1771-1782
- Moilanen A (2011) On the limitations of graph-theoretic connectivity in spatial ecology and conservation. Journal of Applied Ecology 48(6):1543-1547
- Moilanen A, Smith Andrew T, Hanski I (1998) Long-term dynamics in a metapopulation of the American pika. The American Naturalist 152(4):530-542
- Monson G, Sumner L (1980) The Desert Bighorn, Its Life History, Ecology and Management. University of Arizona Press, Tucson
- Monteith KB, Monteith KL, Bowyer RT, Leslie DM, Jenks JA (2014) Reproductive effects on fecal nitrogen as an index of diet quality: an experimental assessment. Journal of Mammalogy 95(2):301-310
- Mould ED, Robbins CT (1981) Nitrogen metabolism in elk. Journal of Wildlife Management 45(2):323-334
- Mysterud A, Yoccoz NG, Langvatn R, Pettorelli N, Stenseth NC (2008) Hierarchical path analysis of deer responses to direct and indirect effects of climate in northern forest. Philosophical Transactions of the Royal Society B: Biological Sciences 363(1501):2357-2366
- Nickerson BS (2014) Effects of genetic drift, natural selection, and population connectivity on adaptive-linked genetic diversity of desert bighorn sheep. Master's thesis, Oregon State University, Corvallis
- Nicotra AB, Beever EA, Robertson AL, Hofmann GE, O'Leary J (2015) Assessing the components of adaptive capacity to improve conservation and management efforts under global change. Conservation Biology 29(5):1268-1278
- Noy-Meir I (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4(1):25-51
- Oakleaf JR, Kennedy CM, Baruch-Mordo S et al (2015) A world at risk: aggregating development trends to forecast global habitat conversion. PLoS ONE 10(10):e0138334
- Opsahl T, Agneessens F, Skvoretz J (2010) Node centrality in weighted networks: generalizing degree and shortest paths. Social Networks 32(3):245-251
- Pannell JR, Charlesworth B (2000) Effects of metapopulation processes on measures of genetic diversity. Philosophical Transactions of the Royal Society B: Biological Sciences 355(1404):1851-1864
- Papouchis CM, Singer FJ, Sloan WB (2001) Responses of desert bighorn sheep to increased human recreation. Journal of Wildlife Management 65(3):573-582
- Parker KL, Barboza PS, Gillingham MP (2009) Nutrition integrates environmental responses of ungulates. Functional Ecology 23(1):57-69
- Parks SA, McKelvey KS, Schwartz MK (2012) Effects of weighting schemes on the identification of wildlife corridors generated with least-cost methods. Conservation Biology:145-154
- Parmesan C (2006) Ecological and evolutionary responses to recent climate change. Annual Review of Ecology, Evolution, and Systematics 37:637-669
- Pascual-Hortal L, Saura S (2006) Comparison and development of new graph-based landscape connectivity indices: towards the priorization of habitat patches and corridors for conservation. Landscape Ecology 21(7):959-967
- Pearson RG, Dawson TP (2003) Predicting the impacts of climate change on the distribution of species: are bioclimate envelope models useful? Global Ecology and Biogeography 12(5):361-371
- Pentry JM, Henry HM, Ede AJ, Crawford AM (1993) Ovine microsatellites at the OarAE16, OarAE54, OarAE57, OarAE119, and OarAE129 loci. Animal Genetics 24(3):219

- Perez-Espona S, Perez-Barberia FJ, McLeod JE, Jiggins CD, Gordon IJ, Pemberton JM (2008) Landscape features affect gene flow of Scottish Highland red deer (*Cervus elaphus*). Molecular Ecology 17(4):981-996
- Pettorelli N, Pelletier F, Hardenberg Av, Festa-Bianchet M, Côté SD (2007) Early onset of vegetation growth vs. rapid green-up: impacts on juvenile mountain ungulates. Ecology 88(2):381-390
- Pettorelli N, Ryan S, Mueller T, Bunnefeld N, Jedrzejewska B, Lima M, Kausrud K (2011) The Normalized Difference Vegetation Index (NDVI): unforeseen successes in animal ecology. Climate Research 46(1):15-27
- Phillips PC (2008) Epistasis the essential role of gene interactions in the structure and evolution of genetic systems. Nature Reviews Genetics 9(11):855-867
- Pigllucci M (1996) How organisms respond to environmental changes: from phenotypes to molecules (and vice versa). Trends in Ecology & Evolution 11(4):168-173
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Development Core Team (2011) nlme: Linear and Nonlinear Mixed Effects Models.
- Pritchard JK, Stephens M, Donnelly P (2000) Inference of population structure using multilocus genotype data. Genetics 155(2):945-959
- Prunier JG, Kaufmann B, Fenet S et al (2013) Optimizing the trade-off between spatial and genetic sampling efforts in patchy populations: towards a better assessment of functional connectivity using an individual-based sampling scheme. Molecular Ecology 22(22):5516-5530
- Pulido F, Berthold P (2004) Microevolutionary response to climatic change. Advances in Ecological Research 35:151-183
- Pulliam HR (1988) Sources, sinks, and population regulation. American Naturalist 132(5):652-661
- R Development Core Team (2014) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Rapacciuolo G, Maher SP, Schneider AC, Hammond TT, Jabis MD, Walsh RE, Iknayan KJ, Walden GK, Oldfather MF, Ackerly DD (2014) Beyond a warming fingerprint: individualistic biogeographic responses to heterogeneous climate change in California. Global Change Biology 20(9):2841-2855
- Rauch EM, Bar-Yam Y (2004) Theory predicts the uneven distribution of genetic diversity within species. Nature 431(7007):449-452
- Rasmussen HB, Wittemyer G, Douglas-Hamilton I (2006) Predicting time-specific changes in demographic processes using remote-sensing data. Journal of Applied Ecology 43(2):366-376
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86(3):248-249
- Réale D, McAdam AG, Boutin S, Berteaux D (2003) Genetic and plastic responses of a northern mammal to climate change. Proceedings of the Royal Society B 270(1515):591-596
- Rebaudo F, Le Rouzic A, Dupas S, Silvain J-F, Harry M, Dangles O (2013) SimAdapt: an individual-based genetic model for simulating landscape management impacts on populations. Methods in Ecology and Evolution 4(6):595-600
- Reed DH, Frankham R (2001) How closely correlated are molecular and quantitative measures of genetic variation? A meta-analysis. Evolution 55(6):1095-1103

- Reed DH, Frankham R (2003) Correlation between fitness and genetic diversity. Conservation Biology 17(1):230-237
- Reed TE, Schindler DE, Waples RS (2011) Interacting effects of phenotypic plasticity and evolution on population persistence in a changing climate. Conservation Biology 25(1):56-63
- Ricketts TH (2001) The matrix matters: effective isolation in fragmented landscapes. American Naturalist 158(1):87-99
- Rioux Paquette S, Talbot B, Garant D, Mainguy J, Pelletier F (2014) Modelling the dispersal of the two main hosts of the raccoon rabies variant in heterogeneous environments with landscape genetics. Evolutionary Applications 7(7):734-749
- Risenhoover KL, Bailey JA (1985) Foraging ecology of mountain sheep: implications for habitat management. Journal of Wildlife Management 49(3):797-804
- Robledo C, Kanninen M, Pedroni L (2005) Tropical forests and adaptation to climate change: in search of synergies. Center for International Forestry Research, Bogor, Indonesia
- Rominger EM, Whitlaw HA, Weybright DL, Dunn WC, Ballard WB (2004) The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68(4):993-999
- Roug A, Gonzales B, Wolff P, Abella R, Torres S, Besser T, Dekelaita D, Powers J, Bleich V, Epps C (in preparation) Respiratory disease in desert bighorn sheep (*Ovis canadensis nelsoni*) of the Mojave desert, California and Nevada
- Rozenfeld AF, Arnaud-Haond S, Hernández-García E, Eguíluz VM, Serrão EA, Duarte CM (2008) Network analysis identifies weak and strong links in a metapopulation system. Proceedings of the National Academy of Sciences 105(48):18824-18829
- Rubin ES, Boyce WM, Caswell-Chen EP (2002) Modeling demographic processes in an endangered population of bighorn sheep. Journal of Wildlife Management 66(3):796-810
- Rubin ES, Boyce WM, Stermer CJ, Torres SG (2002) Bighorn sheep habitat use and selection near an urban environment. Biological Conservation 104(2):251-263
- Ryan SJ, Cross PC, Winnie J, Hay C, Bowers J, Getz WM (2012) The utility of normalized difference vegetation index for predicting African buffalo forage quality. Journal of Wildlife Management 76(7):1499-1508
- Santin-Janin H, Garel M, Chapuis J-L, Pontier D (2009) Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: a case study on the Kerguelen archipelago. Polar biology 32(6):861-871
- Saunders DA, Hobbs RJ, Margules CR (1991) Biological consequences of ecosystem fragmentation: a review. Conservation Biology 5(1):18-32
- Sawyer SC, Epps CW, Brashares JS (2011) Placing linkages among fragmented habitats: do least-cost models reflect how animals use landscapes? Journal of Applied Ecology 48(3):668-678
- Schaeffer R, Torres S, Bleich V (2000) Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. California Fish and Game 86(2):127-135
- Schloss CA, Nuñez TA, Lawler JJ (2012) Dispersal will limit ability of mammals to track climate change in the Western Hemisphere. Proceedings of the National Academy of Sciences 109(22):8606-8611

- Schoville SD, Bonin A, François O, Lobreaux S, Melodelima C, Manel S (2012) Adaptive genetic variation on the landscape: methods and cases. Annual Review of Ecology, Evolution, and Systematics 43(1):23-43
- Schwalm D, Epps CW, Rodhouse TJ et al (2015) Habitat availability and gene flow influence diverging local population trajectories under scenarios of climate change: a place-based approach. Global Change Biology, doi: 10.1111/gcb.13189
- Schwartz MK, Copeland JP, Anderson NJ et al (2009) Wolverine gene flow across a narrow climatic niche. Ecology 90(11):3222-3232
- Schwartz OA, Bleich VC, Holl SA (1986) Genetics and the conservation of mountain sheep *Ovis canadensis nelsoni*. Biological Conservation 37(2):179-190
- Seager R, Ting M, Held I, Kushnir Y, Lu J, Vecchi G, Huang H-P, Harnik N, Leetmaa A, Lau N-C, Li C, Velez J, Naik N (2007) Model projections of an imminent transition to a more arid climate in southwestern North America. Science 316(5828):1181-1184
- Seager R, Ting M, Li C, Naik N, Cook B, Nakamura J, Liu H (2013) Projections of declining surface-water availability for the southwestern United States. Nature Climate Change 3(5):482-486
- Sesnie SE, Dickson BG, Rosenstock SS, Rundall JM (2011) A comparison of Landsat TM and MODIS vegetation indices for estimating forage phenology in desert bighorn sheep (*Ovis canadensis nelsoni*) habitat in the Sonoran Desert, USA. International Journal of Remote Sensing 33(1):276-286
- Shirk AJ, Wallin DO, Cushman SA, Rice CG, Warheit KI (2010) Inferring landscape effects on gene flow: a new model selection framework. Molecular Ecology 19(17):3603-3619
- Shoemaker DD, Jaenike J (1997) Habitat continuity and the genetic structure of Drosophila populations. Evolution 51(4):1326-1332
- Short Bull RA, Cushman SA, Mace R, Chilton T, Kendall KC, Landguth EL, Schwartz MK, McKelvey K, Allendorf FW, Luikart G (2011) Why replication is important in landscape genetics: American black bear in the Rocky Mountains. Molecular Ecology 20(6):1092-1107
- Skelly DK, Joseph LN, Possingham HP, Freidenburg LK, Farrugia TJ, Kinnison MT, Hendry AP (2007) Evolutionary responses to climate change. Conservation Biology 21(5):1353-1355
- Simberloff D, Cox J (1987) Consequences and costs of conservation corridors. Conservation Biology 1(1):63-71
- Singer FJ, Gudorf MA (1999) Restoration of bighorn sheep metapopulations in and near 15 national parks: conservation of a severely fragmented species. Volume I: planning, problem definition, key findings, and restoration. U.S. Geological Survey and U.S. Department of the Interior, Open File Report 99-102
- Slatkin M (1976) The rate of spread of an advantageous allele in a subdivided population. In: Karlin S, Nevo E (eds) Population Genetics and Ecology. Academic Press, New York
- Smith SJ, Edmonds J, Hartin CA, Mundra A, Calvin K (2015) Near-term acceleration in the rate of temperature change. Nature Climate Change 5(4):333-336

- Smith TP, Lopez-Corrales N, Grosz MD, Beattie CW, and Kappes SM (1997) Anchoring of bovine chromosomes 4, 6, 7, 10, and 14 linkage group telomeric ends via FISH analysis of lambda clones. Mammalian Genome 8(5):333-336
- Sniezko RA (2006) Resistance breeding against nonnative pathogens in forest trees current successes in North America. Canadian Journal of Plant Pathology 28(S1):S270-S279
- Sork VL, Waits L (2010) Contributions of landscape genetics approaches, insights, and future potential. Molecular Ecology 19(17):3489-3495
- Soulé M (1976) Allozyme variation: its determinants in space and time. In: Ayala FJ (ed), Molecular Evolution. Sinauer Associates, Sunderland, MA
- Spear SF, Balkenhol N, Fortin M-J, McRae BH, Scribner KIM (2010) Use of resistance surfaces for landscape genetic studies: considerations for parameterization and analysis. Molecular Ecology 19(17):3576-3591
- Spielman D, Brook B, Briscoe D, Frankham R (2004) Does inbreeding and loss of genetic diversity decrease disease resistance? Conservation Genetics 5(4):439-448
- Steffen P, Eggen A, Stranzinger G, Fries R, Dietz A, Womack J (1993) Isolation and mapping of polymorphic microsatellites in cattle. Animal Genetics 24(2):121-124
- Steiner CC, Weber JN, Hoekstra HE (2007) Adaptive variation in beach mice produced by two interacting pigmentation genes. PLoS Biol 5(9):e219
- Stockwell CA, Hendry AP, Kinnison MT (2003) Contemporary evolution meets conservation biology. Trends in Ecology & Evolution 18(2):94-101
- Summers DM, Bryan BA, Crossman ND, Meyer WS (2012) Species vulnerability to climate change: impacts on spatial conservation priorities and species representation. Global Change Biology 18(7):2335-2348
- Swarbrick P, Buchanan F, Crawford A (1991) Ovine dinucleotide repeat polymorphism at the MAF35 locus. Animal Genetics 22(4):369-370
- Tan B, Masek JG, Wolfe R, Gao F, Huang C, Vermote EF, Sexton JO, Ederer G (2013) Improved forest change detection with terrain illumination corrected Landsat images. Remote Sensing of Environment 136(0):469-483
- Taylor PD, Fahrig L, Henein K, Merriam G (1993) Connectivity is a vital element of landscape structure. Oikos 68(3):571-573
- Teillet PM, Staenz K, William DJ (1997) Effects of spectral, spatial, and radiometric characteristics on remote sensing vegetation indices of forested regions. Remote Sensing of Environment 61(1):139-149
- Theobald DM, Reed SE, Fields K, Soulé M (2012) Connecting natural landscapes using a landscape permeability model to prioritize conservation activities in the United States. Conservation Letters 5(2):123-133
- Thomas CD (2005) Recent evolutionary effects of climate change. In: Lovejoy TE, Hannah L (eds), Climate Change and Biodiversity, Yale University Press, New Haven, Connecticut
- Thomas CD, Cameron A, Green RE et al (2004) Extinction risk from climate change. Nature 427(6970):145-148
- Torres SG, Bleich VC, Wehausen JD (1994) Status of bighorn sheep in California, 1993. Desert Bighorn Council Transactions 38:17-28
- Trimble M, Ferreira S, Van Aarde R (2009) Drivers of megaherbivore demographic fluctuations: inference from elephants. Journal of Zoology 279(1):18-26

- Turner MG, Gardner RH, O'Neill RV (2001) Landscape Ecology in Theory and Practice: Pattern and Process. Springer Science+Business Media, New York
- Urban DL, Minor ES, Treml EA, Schick RS (2009) Graph models of habitat mosaics. Ecology Letters 12(3):260-273
- U.S. Bureau of Land Management (2015) Soda Mountain Solar Project Final Environmental Impact Statement. Barstow Field Office, Barstow, CA
- U.S. Bureau of Land Management, U.S. Department of Energy (2012) Final programmatic environmental impact statement (PEIS) for solar energy development in six southwestern states : executive summary.
- U.S. Congress (1916) The National Park Service Organic Act. 16 U.S.C. 1, 2, 3, and 4.
- Utah Division of Wildlife Resources (2013) Utah bighorn sheep statewide management plan. Utah Department of Natural Resources.
- Valdez R, Krausman PR (1999) Mountain Sheep of North America. University of Arizona Press, Tucson
- Valière N (2002) GIMLET: a computer program for analysing genetic individual identification data. Molecular ecology notes 2(3):377-379
- Valladares F, Gianoli E, Gómez JM (2007) Ecological limits to plant phenotypic plasticity. New Phytologist 176(4):749-763
- Vandergast AG, Bohonak AJ, Hathaway SA, Boys J, Fisher RN (2008) Are hotspots of evolutionary potential adequately protected in southern California? Biological Conservation 141(6):1648-1664
- van Etten J (2012) gdistance: distances and routes on geographical grids. R package version 1.1-4
- Varvio S-L, Chakraborty R, Nei M (1986) Genetic variation in subdivided populations and conservation genetics. Heredity 57(2):189-198
- Visser ME (2008) Keeping up with a warming world; assessing the rate of adaptation to climate change. Proceedings of the Royal Society B 275(1635):649-659
- Wallace CS, Thomas KA (2008) An annual plant growth proxy in the Mojave Desert using MODIS-EVI data. Sensors 8(12):7792-7808
- Wallace CS, Webb RH, Thomas KA (2008) Estimation of perennial vegetation cover distribution in the Mojave Desert using MODIS-EVI data. GIScience & Remote Sensing 45(2):167-187
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJC, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. Nature 416(6879):389-395
- Warren MS, Hill JK, Thomas JA, Asher J, Fox R, Huntley B, Roy DB, Telfer MG, Jeffcoate S, Harding P, Jeffcoate G, Willis SG, Greatorex-Davies JN, Moss D, Thomas CD (2001) Rapid responses of British butterflies to opposing forces of climate and habitat change. Nature 414(6859):65-69
- Weber K (1990) Increased selection response in larger populations. I. Selection for wingtip height in *Drosophila melanogaster* at three population sizes. Genetics 125(3):579-584
- Weeks AR, Sgro CM, Young AG, Frankham R, Mitchell NJ, Miller KA, Byrne M, Coates DJ, Eldridge MDB, Sunnucks P, Breed MF, James EA, Hoffman AA (2011) Assessing the benefits and risks of translocations in changing environments: a genetic perspective. Evolutionary Applications 4(6):709-725

- Wasserman TN, Cushman SA, Littell JS, Shirk AJ, Landguth EL (2012) Population connectivity and genetic diversity of American marten (*Martes americana*) in the United States northern Rocky Mountains in a climate change context. Conservation Genetics:1-13
- Wehausen J (1992)The role of precipitation and temperature in the winter range diet quality of mountain sheep of the Mount Baxter herd, Sierra Nevada. Biennial Symposium of the North American Wild Sheep and Goat Council 8:279-292
- Wehausen J (2005) Nutrient predictability, birthing seasons, and lamb recruitment for desert bighorn sheep. In: Goerrissen J (ed), Symposium Proceedings for the Sweeney Granite Mountains Desert Research Center 1978–2003; A Quarter Century of Research and Teaching. University of California Natural Reserve Program, Riverside, CA
- Wehausen JD (1995) Fecal measures of diet quality in wild and domestic ruminants. The Journal of Wildlife Management 59(4):816-823
- Wehausen JD (1996) Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24(3):471-479
- Wehausen JD (1999) Rapid extinction of mountain sheep populations revisited. Conservation Biology 13(2):378-384
- Wehausen JD, Bleich VC, Blong B, Russi TL (1987) Recruitment dynamics in a Southern California mountain sheep population. Journal of Wildlife Management 51(1):86-98
- Wehausen JD, Kelley ST, Ramey RR (2011) Domestic sheep, bighorn sheep, and respiratory disease: a review of the experimental evidence. California Fish and Game 97(1):7-24
- Wehausen JD, Ramey RR (2000) Cranial morphometric and evolutionary relationships in the northern range of *Ovis canadensis*. Journal of Mammalogy 81(1):145-161
- Wehausen JD, Ramey RR, Epps CW (2004) Experiments in DNA extraction and PCR amplification from bighorn sheep feces: the importance of DNA extraction method. Journal of Heredity 95(6):503-50Whitlock MC (2003) Fixation probability and time in subdivided populations. Genetics 164(2):767-779
- Whiting JC, Bowyer RT, Flinders JT, Eggett DL (2011) Reintroduced bighorn sheep: fitness consequences of adjusting parturition to local environments. Journal of Mammalogy 92(1):213-220
- Whitlock MC, McCauley DE (1999) Indirect measures of gene flow and migration:  $F_{ST} \neq 1/(4Nm+1)$ . Heredity 82(2):117-125
- Whittaker DG, Ostermann SD, Boyce WM, DeWoody (2004) Genetic variability of reintroduced California bighorn sheep in Oregon. Journal of Wildlife Management 68(4):850-859
- Wiedmann BP, Sargeant GA (2014) Ecotypic variation in recruitment of reintroduced bighorn sheep: implications for translocation. Journal of Wildlife Management 78(3):394-401
- Willi Y, van Buskirk J, Hoffmann AA (2006) Limits to the adaptive potential of small populations. Annual Review of Ecology, Evolution, and Systematics 37:433-458

- Williams SE, Shoo LP, Isaac JL, Hoffmann AA, Langham G (2008) Towards an integrated framework for assessing the vulnerability of species to climate change. PLoS Biology 6(12):e325
- Wilson L, Blaisdell J, Welsh G, Weaver R, Brigham R, Kelly W, Yoakum J, Hinks M, Turner J, DeForge J (1980) Desert bighorn habitat requirements and management recommendations. Desert Bighorn Council Transactions 24(1):7
- Wittemyer G, Barner Rasmussen H, Douglas-Hamilton I (2007) Breeding phenology in relation to NDVI variability in free-ranging African elephant. Ecography 30(1):42-50
- Worthington Wilmer J, Elkin C, Wilcox C, Murray L, Niejalke D, Possingham H (2008) The influence of multiple dispersal mechanisms and landscape structure on population clustering and connectivity in fragmented artesian spring snail populations. Molecular Ecology 17(16):3733-3751
- Wright S (1969) Evolution and the Genetics of Populations: Vol. 2. The Theory of Gene Frequencies. University of Chicago Press, Chicago, Illinois
- Yamamichi M, Innan H (2012) Estimating the migration rate from genetic variation data. Heredity 108(4):362-363
- Young A, Boyle T, Brown T (1996) The population genetic consequences of habitat fragmentation for plants. Trends in Ecology & Evolution 11(10):413-418
- Zeller K, Creech T, Millette K, Crowhurst R, Long R, Wagner H, Balkenhol B, Landguth E (*in review*) Using simulations to evaluate Mantel-based methods for assessing landscape resistance to gene flow. Molecular Ecology
- Zeller K, McGarigal K, Whiteley A (2012) Estimating landscape resistance to movement: a review. Landscape Ecology 27(6):777-797

APPENDICES

# **APPENDIX A: PATCH NAMES AND ABBREVIATIONS FOR CHAPTER 1**

Patch name	Abbreviation	Patch name	Abbreviation
Argus Mtns	ARG	Nopah Mtns	NOP
Avawatz Mtns	AVA	North Bristol Mtns	NBR
Big Maria Mtns	BMA	North San Bernardino/ Cushenbury Mtns	NSB
Black Mts/ Greenwater Range	BGR	North Soda Mtns	NSO
Bullion Mtns	BUL	North Spring Range	NSP
Cady Mtns	CAD	Old Dad Peak/ Kelso Mtns/ Marl Mtns/ Club Peak/ Indian Spring	ОКМ
Cargo Muchacho Mtns	CAR	Old Woman Mtns	OWO
Chemehuevi Mtns	CHE	Orocopia Mtns	ORO
Chuckwalla Mtns	CHU	Owlshead Mtns	OWL
Clark Mtns/ South Spring Range	CSS	Palen Mtns/ Riverside Granite Mtns	PRG
Clipper Mtns	CLI	Panamint Mtns	PAN
Coxcomb Mtns	COX	Pinto Mtns	PIN
Dead Mtns	DEA	Piute Mtns	PIU
Eagle Crags	ECR	Piute Range/ Castle Peaks/ Castle Mtns	PCC
Eagle Mtns	EMO	Providence Mtns	PRO
East Chocolate Mtns	ECH	Quail Mtns	QUA
Eldorado Mtns	EDO	Queen Mtn	QUE
Ft. Irwin Granite Mtns	FIG	Riverside Mtns	RIV
Granite Mtns	GRA	Sacramento Mtns	SAC
Highland Range/ McCullough Range	НМС	San Gabriel Mtns	SGA
Iron Mtns	IRO	San Gorgonio Mtns	SGO
Kingston Mtns/ Mesquite Mtns	KME	Sheephole Mtns	SHE
Little Maria Mtns	LMA	Slate Range	SLA
Little San Bernardino Mtns	LSB	South Bristol Mtns	SBR
Marble Mtns	MAR	South Soda Mtns	SSO
McCoy Mtns	MCY	Turtle Mtns	TUR
Mescal Range/ Ivanpah Mtns	MIV	West Chocolate Mtns	WCH
Newberry Mtns	NNV	Whipple Mtns	WHI
Newberry Mtns/ Ord Mtns/ Rodman Mtns	NOR	Woods Mtns/ Hackberry Mtns	WHA

Table A.1. Names and abbreviations of desert bighorn habitat patches included in Chapter 1. Buffer patches are italicized.

# APPENDIX B: CONSTRUCTING GENETIC AND DEMOGRAPHIC NETWORKS

#### Calculating least-cost path effective distances

We generated least-cost paths (LCPs) between all pairs of habitat patches using the Distance tools in the Spatial Analyst extension for ArcGIS 10.0 (ESRI, Redlands, CA). The input data for this analysis included:

- Habitat patches: a vector layer denoting the boundaries of desert bighorn sheep habitat polygons, including populated, unpopulated, and "buffer" habitat patches. We established polygon boundaries using expert opinion based on topography and known sheep distribution; in previous analyses, expert opinion polygons performed equally well as more complicated habitat model-based polygons (Epps et al. 2007).
- 2. Landscape resistance: a raster layer of values denoting the relative cost of moving through each landscape cell. We created this layer via the following steps:
  - a. Starting with a 1-arcsecond resolution digital elevation model (DEM) of the study area, we used the AGGREGATE tool to create a 3-arcsecond (approximately 90-m) resolution DEM.
  - b. We used the SLOPE tool to create a new raster layer of percent slope values, with the 3-arcsecond DEM as the input.
  - c. We used the RECLASSIFY tool to create a new raster layer of landscape resistance value based on percent slope. Cells of >15% slope were assigned cost value of 1; cells of ≤15% slope were assigned cost value of 10.
  - d. We added barrier features to the landscape resistance raster. We used the MASK tool to convert a vector layer of barrier features (interstate highways, canals, urban areas, etc.) to a raster layer in which cells overlapping barrier features were assigned a value of 10 million, and all other cells were classified as NO DATA. We then used the RASTER CALCULATOR tool to create a new landscape resistance layer in which barrier cells (with cost value = 10 million) were overlain on original landscape resistance cells (with cost value = 1 or 10, depending on slope).

We used the landscape resistance raster layer and the habitat polygons vector layer as inputs to the COSTPATH and COSTDISTANCE tools, which we used to calculate the least-cost path between each pair of habitat patches. We used the cost distances of these LCPs as pairwise effective distances (ED) when modeling the relationship between genetic distance and ED among pairs of patches. Additionally, we repeated this analysis using a landscape resistance raster layer without barriers. We used the cost distances between habitat patches under the no-barriers scenario to determine which pairs would be connected by  $\langle ED_{MAX}$  if current barriers were removed (i.e., which currently-severed dispersal corridors would be suitable candidates for restoration).

#### **Creating networks**

We inferred genetic (i.e. male-mediated) connectivity between pairs of habitat patches using a model of the relationship between least-cost path ED and genetic distance ( $F_{ST}$ ) fit with data from a sample of habitat patch pairs in the study area. This analysis was previously published in Epps et al. (2007). The genetic dataset included 392 individuals from 26 populations genotyped at 14 microsatellite loci. Pairwise  $F_{ST}$  values were calculated in ARLEQUIN and transformed to Nm values using the Wright-Fisher model  $F_{ST} = 1/(1 + 4Nm)$ . The following model was derived from the regression of Nm values on ED values:

$$Nm = 9.141 * e^{-0.112*ED} - 0.219$$

Epps et al. (2007) estimated a maximum effective dispersal distance of 16.4 resistance units (called "km-cost-units" in Epps et al. 2007; see Fig. 3 from that paper) from this relationship.

We used a combination of radio telemetry records and mitochondrial haplotype data to estimate  $ED_{MAX}$  for females. We found nine records of radio-collared ewes dispersing between patches. Our haplotype dataset included 515-b.p. sequences from the mitochondrial control region in 394 individuals from 27 populations (Epps et al. 2005; Epps et al. 2010). A haplotype that is shared between two patches is evidence of female dispersal between these patches because mtDNA is maternally inherited and cannot be transferred by dispersing males. We only used haplotype data from females (sex was determined genetically; Epps et al. 2010) in this analysis because first-generation migrant males could have haplotypes inherited from mothers in different patches, in which case a

shared haplotype with another patch would not necessarily indicate female dispersal from that patch. We inferred 22 female dispersal events based on haplotype sharing, considering only those instances in which direct dispersal between patches was the most plausible pathway (as opposed to indirect dispersal between patches via a series of shorter steps through intermediary patches).

For each dispersal event, we calculated the ED of the least-cost path between the source and destination patches using the procedure outlined above. Figure B.1 shows the frequency distribution of the EDs of these ewe dispersal events. Ewe dispersal events were restricted to within approximately 10 resistance units; two shared haplotypes were observed at greater distances, but because there are other possible explanations for haplotype sharing between those populations, we chose to treat them as outliers. The shape of this frequency distribution is similar to the negative binomial relationship for Nm vs. ED found by Epps et al. (2007). We assumed that the female Nm-ED relationship exhibited the same general shape, and shifted the intercept of the negative binomial relationship in Epps et al. (2007) downward such that the new ED<sub>MAX</sub> value was 10 km-cost-units (Fig. B.2). The resulting equation for female dispersal was:

Nm = 9.141 \* e-0.112\*ED - 1.74512

Because our estimate of female EDMAX was a rough approximation, we explored the sensitivity of our results to errors as large as 30 percent (see Appendix C).



Figure B.1. Histogram of effective distances of known ewe dispersal events.



effective distance (resistance units)

Figure B.2. Estimated relationships between *Nm* and effective distance for males and females. Dashed horizontal line shows the value of *Nm* beyond which additional effective distance does not lead to further decline in *Nm*.

#### **Removing redundant links**

Because our resistance model identifies steeply sloped areas as lowest resistance, and habitat patches are large areas of steeply sloped habitat, least-cost paths between distant patches often travel through intervening patches. This means that multiple network corridors may represent the same geographical path, and creates the potential for redundancy in the network. Overlapping least-cost paths present a problem when trying to evaluate the individual effects of corridors on network-level connectivity, because some corridors cannot be removed independently of all other corridors. Figure B.3 presents an example of this situation in the Mojave bighorn system: traveling along the least-cost path between the Granite Mountains (GRA) and Wood/Hackberry Mountains (WHA) is roughly equivalent to traveling along two shorter least-costs paths, from GRA to the Providence Mountains (PRO) and then from PRO to WHA. If all three of these least-cost paths (GRA--PRO, PRO--WHA, GR--WHA) are represented as corridors in the network, we introduce redundancy because the least-cost path associated with the GRA--WHA corridor is composed of the two shorter least-cost paths associated with the GRA--PRO and PRO--WHA corridors. It makes little biological sense to evaluate the effect of losing connectivity along the GRA-PRO least-cost path (e.g., a highway constructed between these patches) unless we also assume that connectivity along the GRA--WHA least-cost path would be lost. If we remove the redundant corridor (GRA-WHA) from our network, we still preserve the connectivity between the GRA and WHA patches in the network (via two shorter corridors), and we now can evaluate the independent effect of losing connectivity along either component of the GRA-WHA least-cost path.

We used a GIS analysis to identify and exclude redundant corridors from the demographic and genetic networks:

- 1. Each patch was buffered by 1 km to reduce sensitivity to patch boundary definition.
- 2. Least-cost paths that intersected one or more buffered occupied patches (other than the source or destination patch for that particular LCP) were identified as redundant.
- 3. Redundant corridors were removed from networks.



Figure B.3. An example of a redundant edge in the Mojave bighorn network. The Granite-Wood/Hackberry least-cost path (dashed line) largely overlaps the two shorter least costs paths (Granite-Providence and Providence-Wood/Hackberry; solid lines) and thus was not included in the network.

# References

- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Epps CW, Wehausen JD, Palsbøll PJ, McCullough DR (2010) Using genetic tools to track desert bighorn sheep colonizations. Journal of Wildlife Management 74(3):522-531

#### **APPENDIX C: SENSITIVITY ANALYSIS**

Male and female  $ED_{MAX}$  are important parameters in our network model but are estimated with error. To explore how error might affect our prioritization results, we performed a simple sensitivity analysis. We tested sensitivity to  $ED_{MAX}$  by increasing or decreasing our estimate by up to 30 percent in 5-percent increments; we then recreated the network and reevaluated the importance of existing and restorable patches and corridors. For each type of management action (patch protection, corridor protection, patch restoration, or corridor restoration), we calculated the Spearman correlation between our original metric values and the new metric values calculated at each new  $ED_{MAX}$  value.

In many cases, the set of patches or corridors considered possible targets for a particular management action (i.e., the "feature set") depended on the value of ED<sub>MAX</sub>; for instance, an empty patch that is located 15 resistance units away from the nearest occupied patch would be considered part of the original feature set for patch restoration in the genetic network (since it is  $\langle ED_{MAX} \rangle$  of 16.4 resistance units from an occupied patch); however, if  $ED_{MAX}$  were reduced to 14 resistance units, that same empty patch would be excluded from the new feature set for patch restoration as it would no longer be  $\langle ED_{MAX} \rangle$  from the nearest occupied patch. In such cases where the original and new feature sets were not equivalent, we calculated the correlation coefficient using metric values for only those features common to the original and new feature sets. Results of this sensitivity analysis are shown in Fig. C.1.

The correlation of metric values among common features may an incomplete measure of effect of  $ED_{MAX}$  estimate on prioritization results if the composition of feature sets varies strongly with  $ED_{MAX}$ . Thus, we also quantified the change in the composition of the feature set as a function of  $ED_{MAX}$  in two ways. First, we calculated the percentage of features in the original feature set that remained in the new feature set for each new  $ED_{MAX}$  value (Fig. C.2). Second, we calculated the proportion of features in each new feature set that were not present in the original feature set (Fig. C.3). Collectively, these analyses indicate how the scope of possible management actions is affected by the estimate of  $ED_{MAX}$ .



Figure C.1. Sensitivity of prioritization results to error in estimated  $ED_{MAX}$  for males (genetic network) and females (demographic network). Lines show Spearman correlation of ECP values or MWC values between the original network and the error network as a function of error level.



Figure C.2. Proportion of the original feature set remaining in the new feature set as a function of  $ED_{MAX}$  in the genetic network (left) and demographic network (right). The feature set is the group of patches or corridors considered possible targets for a particular management action, which may vary with  $ED_{MAX}$ . Results for patch protection are not shown because the set of currently occupied patches does not vary with  $ED_{MAX}$ .



Figure C.3. Proportion of the new feature set that is absent from the original feature set as a function of  $ED_{MAX}$  in the genetic network (left) and demographic network (right). The feature set is the group of patches or corridors considered possible targets for a particular management action, which may vary with  $ED_{MAX}$ . Results for patch protection are not shown because the set of currently occupied patches does not vary with  $ED_{MAX}$ .

#### **APPENDIX D: NETWORK METRICS**

We used two global network metrics to evaluate the effects of individual patches and corridors on network connectivity. We formulated the first metric, effectively connected pairs (ECP), as a simple measure of the extent of connectivity among patches that are within the ED range of a single dispersal event. This metric reflects the potential for short-term connectivity within the network. We used the *shortest.paths* function in the *igraph* package for R (Csardi and Nepusz 2006) to identify the shortest path between each pair of patches, then calculated the combined ED of each shortest path (i.e., the sum of the EDs of all corridors included in the shortest path) and counted the number of shortest paths that had combined ED < ED<sub>MAX</sub>.

The second metric, mean weighted closeness (MWC), estimates how close every patch is to every other patch in a network and accounts for weight differences among corridors. This metric reflects the potential for long-term connectivity within the network. We calculated the weighted closeness of each patch *i* as

$$\sum_{j} \frac{1}{d_{ij}}$$

where  $d_{ij}$  was the weighted distance between patches *i* and *j*. In our case,  $d_{ij}$  was calculated using Dijkstra's algorithm: we inverted the *Nm*-based edge weights, then calculated  $d_{ij}$  as the sum of these inverse weights along the shortest path (i.e., smallest sum) between *i* and *j*. If there was no path connecting *i* and *j*, then  $d_{ij}$  was assigned a value of infinity. This is a slight departure from the traditional formula for closeness, but has the advantage of being calculable for networks with multiple components (Opsahl et al. 2010). We then calculated the mean of the weighted closeness values of all network patches as a global metric of closeness.

#### References

Csardi G, Nepusz T (2006) The igraph software package for complex network research. InterJournal, Complex Systems 1695:38

Opsahl T, Agneessens F, Skvoretz J (2010) Node centrality in weighted networks: generalizing degree and shortest paths. Social Networks 32(3):245-251

#### **APPENDIX E: TESTING RELEVANCE OF NETWORK METRICS**

We tested the relevance of our network-level metrics (ECP and MWC) by generating patch-level analogs and determining whether they predicted nuclear genetic diversity (allelic richness, A, and expected heterozygosity,  $H_e$ ) and mitochondrial genetic diversity (haplotype richness, HR) of patches in the genetic and demographic networks, respectively. This analysis included 25 patches within the study area for which both nuclear genetic data and mitochondrial DNA haplotypes were available (Epps et al. 2005; Epps et al. 2010); the nuclear genetic data were used to derive the original models of gene flow and landscape resistance (Epps et al. 2007), but those analyses considered genetic difference between populations rather than genetic diversity as used in this analysis. Both A and HR were corrected for sample size by repeatedly resampling alleles or haplotypes from each population using the smallest sample size for any population (n = 6) and averaging the number of alleles or haplotypes observed across those resamples. Our patch-level analog of ECP was the number of patches connected to a single focal patch along a path (single or multi-step) of effective distance  $\langle ED_{MAX}$  (hereafter "ECPp"). Our patch-level analog of MWC was simply the weighed closeness of each patch (hereafter "WCp"), as calculated in Opsahl et al. (2010). We used simple linear regression to test whether A and  $H_e$  were correlated with patch-level metrics calculated from the genetic network, and whether HR was correlated with patch-level metrics calculated from the demographic network. We also ran similar models using two common patch-level centrality metrics, degree and betweenness, as predictor variables in order to compare the explanatory power of our metrics to standard network metrics. Degree is the number of edges attached to a node; betweenness is the number of shortest paths from all nodes to all others that pass through a given node).

### Results

Patch-based analogs of our network metrics calculated for the genetic network predicted both A and  $H_e$  of 25 populations within our study system (Table E.1). Correlations of both genetic diversity indices were slightly stronger with WCp than ECPp, suggesting that long-distance, multiple-step movements among patches influence nuclear genetic diversity beyond what is predicted by the number of populations within ED<sub>MAX</sub> of any given patch. *HR* was strongly predicted by both patch-based analogs calculated for the demographic model. ECPp predicted slightly more variation in *HR* than WCp, suggesting that long-distance, multi-step female movements (captured by WCp) had less detectable influence on *HR* (Table E.1). ECP and MWC both explained considerably more of the variation in all three genetic diversity indices than either degree or betweenness, indicating that our metrics are stronger predictors of male- and female-mediated gene flow than these two traditional metrics (Table E.1).

Table E.1. Linear regression of genetic diversity on patch-level analogs of network metrics used to describe connectivity for desert bighorn sheep populations in the Mojave Desert. Allelic richness and expected heterozygosity were estimated from 14 microsatellite markers and are expected to be affected most strongly by male-mediated gene flow because dispersal in bighorn sheep is sex-biased. Mitochondrial DNA haplotype richness (515 base pairs of control region) is expected to reflect female movements, as mtDNA is maternally inherited.

Type of Genetic Diversity <sup>1</sup>	Network	Patch-level network metric	$R^2$	Р	
Α	Genetic	<sup>2</sup> WCp	0.34	0.002	
Α	Genetic	<sup>3</sup> ECPp	0.24	0.014	
Α	Genetic	degree	0.06	0.223	
Α	Genetic	betweenness	0.01	0.617	
$H_e$	Genetic	WCp	0.31	0.004	
$H_e$	Genetic	ECPp	0.19	0.029	
$H_e$	Genetic	degree	0.04	0.311	
$H_e$	Genetic	betweenness	0.03	0.397	
HR	Demographic	ECPp	0.56	< 0.0001	
HR	Demographic	WCp	0.53	< 0.0001	
HR	Demographic	degree	0.43	0.0004	
HR	Demographic	betweenness	0.32	0.003	

 ${}^{1}A$  = allelic richness,  $H_{e}$  = expected heterozygosity, HR = haplotype richness

<sup>2</sup>Patch-level weighted closeness, a measure of how close a focal patch is to all other network patches along shortest paths, as defined in Opsahl (2010)

<sup>3</sup>Patch-level effectively connected pairs, defined as the number of patches within  $ED_{MAX}$  of a focal patch (including along multi-step pathways of combined effective distance <  $ED_{MAX}$ )

### References

- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
- Opsahl T, Agneessens F, Skvoretz J (2010) Node centrality in weighted networks: generalizing degree and shortest paths. Social Networks 32(3):245-251

#### **APPENDIX F: NETWORK PROPERTIES**

In addition to our ECP and MWC metrics, here we report several common network metrics to facilitate comparison with other ecological networks.

*Clustering coefficient* (also called transitivity) is the probability that a node's neighbors (i.e., directly connected nodes) are themselves neighbors, a measure of the extent to which network nodes tend to cluster together. The global unweighted clustering coefficient was 0.473 for the genetic network and 0.306 for the demographic network. *Degree* is the number of edges connected to a node. The mean unweighted degree was 2.93 for the genetic network and 1.69 for the demographic network.

The *degree distribution* is the distribution of network node's degree values, and is often compared to the degree distribution of random networks with the same number of nodes and edges. The degree distribution of the genetic and demographic networks are compared to average degree distribution of 1000 Erdos-Renyi random networks of the same size in Figure F.1 below.

Other common network metrics (e.g., characteristic patch length) are not calculable for our genetic and demographic networks because they have multiple components (i.e., isolated nodes).



Figure F.1. Degree distribution of the observed network (solid line) versus the average Erdos-Renyi network of the same size (dashed line) for the genetic network (top panel) and the demographic network (bottom panel).

#### **APPENDIX G: PRIORITIZATION RESULTS**

Complete prioritization results from the network analysis for each of four management actions (patch protection, corridor protection, patch restoration, corridor restoration) are shown in Tables G.1-G.4. Features are ordered by  $\Delta$  value (the proportional change in network connectivity when a feature is added or removed from the network; higher  $\Delta$  values indicate more important patches for network connectivity) and ranked accordingly for both network metrics.

For patch protection and patch restoration results, the lowest ranking features by MWC have slightly negative  $\Delta$  values. This should not be interpreted as evidence that these patches are (or would be) harmful to network connectivity; rather, this reflects the peripheral nature of these patches and its influence on MWC. Removing a highly peripheral patch from the network can decrease the average length of shortest paths between pairs of patches in the network, and conversely, adding a highly peripheral patch can increase the average length of shortest paths. This may lead to a negative  $\Delta$  value associated with these patches, but from a practical perspective, protecting or restoring a patch should never be deleterious to connectivity of the network.  $\Delta$  values should therefore be interpreted only as a relative measure of the impact of individual features on connectivity.

Network visualizations of prioritization results for patch restoration and corridor restoration are shown in Figures G.1-G.4.

Table G.1. Prioritization results for patch protection in the genetic and demographic networks based on ECP<sup>a</sup> and MWC<sup>b</sup>. Patches are ranked from highest to lowest importance, with separate rankings for each combination of network type and network metric.

Genetic network					Demographic network						
	ECP			MWC			ECP			MWC	
Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank
PRO	0.205	1	COX	0.162	1	GRA	0.231	1	PRO	0.203	1
GRA	0.180	2	IRO	0.142	2	PRO	0.215	2	GRA	0.190	2
PCC	0.172	3	PRO	0.134	3	NBR	0.200	3	PCC	0.161	3
NBR	0.156	4	OWO	0.130	4	CAD	0.138	4	NBR	0.154	4
CAD	0.115	5	PCC	0.108	5	PCC	0.123	5	CAD	0.105	5
COX	0.082	7	PRG	0.077	6	KME	0.108	6.5	KME	0.099	6
KME	0.082	7	GRA	0.074	7	WHA	0.108	6.5	CSS	0.082	7
SHE	0.082	7	SHE	0.067	8	CSS	0.092	8	WHA	0.064	8
AVA	0.074	9.5	NBR	0.064	9	COX	0.077	11	SHE	0.054	9
WHA	0.074	9.5	EMO	0.054	10	EMO	0.077	11	SSO	0.045	10
CSS	0.066	13	MAR	0.052	11	QUE	0.077	11	EMO	0.038	11
EMO	0.066	13	QUE	0.045	12	SHE	0.077	11	AVA	0.038	12
LSB	0.066	13	KME	0.045	13	SSO	0.077	11	PRG	0.035	13
PRG	0.066	13	LSB	0.044	14	BUL	0.046	16.5	LSB	0.032	14
SSO	0.066	13	CAD	0.044	15	IRO	0.046	16.5	COX	0.031	15
BUL	0.057	17.5	TUR	0.040	16	LSB	0.046	16.5	QUE	0.030	16
IRO	0.057	17.5	BUL	0.039	17	MAR	0.046	16.5	BUL	0.025	17
OKM	0.057	17.5	WHA	0.037	18	OKM	0.046	16.5	IRO	0.025	18
QUE	0.057	17.5	CSS	0.036	19	PRG	0.046	16.5	DEA	0.023	19
OWO	0.049	20	LMA	0.028	20	AVA	0.031	23.5	OKM	0.022	20
SGO	0.041	21	SGO	0.028	21	CHU	0.031	23.5	ORO	0.015	21
DEA	0.033	25	NSB	0.023	22	CLI	0.031	23.5	MAR	0.014	22
ECR	0.033	25	SSO	0.022	23	DEA	0.031	23.5	LMA	0.012	23
LMA	0.033	25	WHI	0.019	24	LMA	0.031	23.5	WCH	0.011	24
MAR	0.033	25	OKM	0.019	25	ORO	0.031	23.5	ECR	0.000	25
NOR	0.033	25	CLI	0.019	26	SBR	0.031	23.5	SBR	0.000	26
NSB	0.033	25	AVA	0.016	27	WCH	0.031	23.5	CLI	-0.001	27
WCH	0.033	25	SBR	0.015	28	ECR	0.015	29.5	NSB	-0.002	28.5
CLI	0.025	29.5	NOR	0.011	29	NSB	0.015	29.5	SGO	-0.002	28.5
ORO	0.025	29.5	DEA	0.011	30	OWO	0.015	29.5	OWO	-0.002	30
CHU	0.016	33	WCH	0.009	31	SGO	0.015	29.5	CHU	-0.005	31
ECH	0.016	33	ORO	0.005	32	CHE	0.000	34.5	CHE	-0.023	34.5
SBR	0.016	33	ECR	0.004	33	ECH	0.000	34.5	ECH	-0.023	34.5
TUR	0.016	33	CHE	-0.003	34	NOR	0.000	34.5	NOR	-0.023	34.5
WHI	0.016	33	CHU	-0.006	35	SGA	0.000	34.5	SGA	-0.023	34.5
CHE	0.008	36	ECH	-0.013	36	TUR	0.000	34.5	TUR	-0.023	34.5
SGA	0.000	37	SGA	-0.023	37	WHI	0.000	34.5	WHI	-0.023	34.5

<sup>a</sup> Effectively connected pairs, a measure of short-term network connectivity. <sup>b</sup> Mean weighted closeness, a measure of long-term network connectivity.

Table G.2. Prioritization results for corridor protection in the genetic and demographic networks based on ECP<sup>a</sup> and MWC<sup>b</sup>. Corridors are ranked from highest to lowest importance, with separate rankings for each combination of network type and network metric.

Genetic network					Demographic network						
ECP			MWC			E	CP		MWC		
Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank
GRA-PRO	0.148	1	IRO-OWO	0.121	1	GRA-NBR	0.169	1	GRA-NBR	0.146	1
GRA-NBR	0.131	2	OWO-TUR	0.055	2	GRA-PRO	0.154	2	CAD-NBR	0.102	2
CAD-NBR	0.098	3	LMA-PRG	0.050	3	CAD-NBR	0.123	3	GRA-PRO	0.091	3
CAD-SSO	0.057	4.5	GRA-PRO	0.047	4	CAD-SSO	0.077	5	CSS-KME	0.084	4
CSS-KME	0.057	4.5	GRA-NBR	0.044	5	CSS-KME	0.077	5	CAD-SSO	0.066	5
BUL-SHE	0.049	6	BUL-SHE	0.040	6	PRO-WHA	0.077	5	BUL-SHE	0.047	6
IRO-PRG	0.033	7.5	TUR-WHI	0.037	7	BUL-SHE	0.046	7.5	IRO-PRG	0.037	7
LMA-PRG	0.033	7.5	MAR-SBR	0.037	8	COX-EMO	0.046	7.5	LMA-PRG	0.034	8
COX-EMO	0.025	10	CAD-NBR	0.034	9	CLI-MAR	0.031	12	PRO-WHA	0.027	9
IRO-OWO	0.025	10	CSS-KME	0.034	10	COX-SHE	0.031	12	COX-EMO	0.024	10
PCC-PRO	0.025	10	COX-EMO	0.028	11	GRA-OKM	0.031	12	ORO-WCH	0.023	11
AVA-ECR	0.016	15.5	IRO-PRG	0.025	12	IRO-PRG	0.031	12	AVA-ECR	0.022	12
BUL-NOR	0.016	15.5	COX-SHE	0.025	13	LMA-PRG	0.031	12	MAR-SBR	0.022	13
CLI-MAR	0.016	15.5	CAD-SSO	0.023	14	MAR-SBR	0.031	12	CLI-MAR	0.021	14
COX-PRG	0.016	15.5	CHE-WHI	0.019	15	QUE-SHE	0.031	12	NSB-SGO	0.020	15
COX-SHE	0.016	15.5	PRO-WHA	0.017	16	AVA-ECR	0.015	20	IRO-OWO	0.020	16
ECH-WCH	0.016	15.5	PCC-PRO	0.016	17	EMO-LSB	0.015	20	PCC-PRO	0.020	17
MAR-SBR	0.016	15.5	ORO-WCH	0.014	18	IRO-OWO	0.015	20	COX-SHE	0.017	18
PRO-WHA	0.016	15.5	COX-IRO	0.013	19	LSB-OUE	0.015	20	LSB-OUE	0.017	19
AVA-KME	0.008	26.5	LSB-OUE	0.011	20	NSB-SGO	0.015	20	PCC-WHA	0.010	20
CHE-WHI	0.008	26.5	NSB-SGO	0.011	21	OKM-PRO	0.015	20	EMO-LSB	0.009	21
CLI-OWO	0.008	26.5	CLI-MAR	0.011	22	ORO-WCH	0.015	20	CHU-ORO	0.006	22
COX-IRO	0.008	26.5	EMO-LSB	0.010	23	PCC-PRO	0.015	20	GRA-OKM	0.004	23
DEA-PCC	0.008	26.5	ECH-WCH	0.009	24	PCC-WHA	0.015	20	OUE-SHE	0.003	24
EMO-LSB	0.008	26.5	OUE-SHE	0.008	25	CHU-ORO	0.000	26	EMO-OUE	0.003	25
LSB-SGO	0.008	26.5	MAR-OWO	0.007	26	CHU-WCH	0.000	26	OKM-PRO	0.003	26
MAR-OWO	0.008	26.5	PCC-WHA	0.007	27	EMO-OUE	0.000	26	CHU-WCH	0.000	27
NSB-SGO	0.008	26.5	BUL-NOR	0.007	28						
OWO-TUR	0.008	26.5	COX-PRG	0.007	29						
ORO-WCH	0.008	26.5	EMO-OUE	0.005	30						
PCC-WHA	0.008	26.5	AVA-ECR	0.005	31						
OUE-SHE	0.008	26.5	OKM-PRO	0.004	32						
TUR-WHI	0.008	26.5	CLI-OWO	0.004	33						
CHU-ORO	0.000	40.5	CHU-ORO	0.004	34						
CHU-WCH	0.000	40.5	LSB-SGO	0.003	35						
COX-OUE	0.000	40.5	NOR-NSB	0.002	36						
EMO-OUE	0.000	40.5	GRA-OKM	0.002	37						
GRA-OKM	0.000	40.5	OUE-SGO	0.002	38						
LSB-NSB	0.000	40.5	NBR-OKM	0.001	39						
LSB-OUE	0.000	40.5	CHU-WCH	0.001	40						
NOR-NSB	0.000	40.5	OKM-SSO	0.001	41						
NOR-SGO	0.000	40.5	DEA-PCC	0.001	42						
NBR-OKM	0.000	40.5	AVA-KME	0.000	43						
NSB-OUE	0.000	40.5	LSB-NSB	0.000	44						
OKM-PRO	0.000	40.5	COX-OUE	0.000	46						
OKM-SSO	0.000	40.5	NOR-SGO	0.000	46						
QUE-SGO	0.000	40.5	NSB-QUE	0.000	46						

<sup>a</sup> Effectively connected pairs, a measure of short-term network connectivity. <sup>b</sup> Mean weighted closeness, a measure of long-term network connectivity.

Table G.3. Prioritization results for patch restoration in the genetic and demographic networks based on ECP<sup>a</sup> and MWC<sup>b</sup>. Patches are ranked from highest to lowest importance, with separate rankings for each combination of network type and network metric.

	Genetic network					Demographic network					
	ECP MWC				ECP		MWC				
Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank	Patch	$\Delta$ value	Rank
PIN	0.098	1	PIN	0.068	1	PIN	0.154	1	PIN	0.082	1
OWL	0.090	2	QUA	0.040	2	QUA	0.108	2.5	OWL	0.072	2
FIG	0.066	3	OWL	0.039	- 3	SLA	0.108	2.5	QUA	0.070	3
MIV	0.057	4.5	SLA	0.036	4	OWL	0.092	4	SLA	0.065	4
SLA	0.057	4.5	FIG	0.030	5	FIG	0.077	5	FIG	0.061	5
QUA	0.049	6	MCY	0.030	6	BMA	0.046	6.5	BMA	0.020	6
BMA	0.041	7	BMA	0.029	7	MCY	0.046	6.5	NSO	0.019	7
MCY	0.033	9	PIU	0.023	8	CAR	0.015	9.5	MCY	0.015	8
NSO	0.033	9	MIV	0.012	9	NSO	0.015	9.5	PIU	0.003	9
PIU	0.033	9	NSO	0.011	10	PIU	0.015	9.5	SAC	-0.007	10
RIV	0.016	11	RIV	0.009	11	SAC	0.015	9.5	CAR	-0.015	11
CAR	0.008	12.5	SAC	0.005	12						
SAC	0.008	12.5	CAR	-0.009	13						

<sup>a</sup> Effectively connected pairs, a measure of short-term network connectivity. <sup>b</sup> Mean weighted closeness, a measure of long-term network connectivity.

Table G.4. Prioritization results for corridor restoration in the genetic and demographic networks based on ECP<sup>a</sup> and MWC<sup>b</sup>. Corridors are ranked from highest to lowest importance, with separate rankings for each combination of network type and network metric.

Genetic network							Den	nograph	nic network		
E	CP		M	WC		ECP MWC				WC	
Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank	Corridor	$\Delta$ value	Rank
GRA-MAR	0.246	1	GRA-MAR	0.342	1	GRA-MAR	0.231	1.5	AVA-SSO	0.196	1
NBR-SBR	0.197	2	NBR-SBR	0.308	2	NBR-SBR	0.231	1.5	GRA-MAR	0.196	2
EMO-ORO	0.123	3	CLI-PRO	0.280	3	LSB-SGO	0.108	3	NBR-SBR	0.185	3
CHU-EMO	0.115	4	BUL-CAD	0.225	4	EMO-ORO	0.092	4	CLI-PRO	0.110	4
CLI-PRO	0.090	5.5	BUL-NBR	0.217	5	CHU-EMO	0.077	5.5	EMO-ORO	0.101	5
LSB-ORO	0.090	5.5	CAD-NOR	0.205	6	LSB-NSB	0.077	5.5	CHU-EMO	0.096	6
ORO-QUE	0.066	7	AVA-CAD	0.171	7	LSB-ORO	0.062	7.5	LSB-SGO	0.094	7
AVA-CAD	0.049	8.5	AVA-SSO	0.166	8	ORO-QUE	0.062	7.5	COX-PRG	0.090	8
AVA-SSO	0.049	8.5	CHE-DEA	0.159	9	NSB-SGA	0.031	9.5	LSB-ORO	0.084	9
ORO-SHE	0.033	10	EMO-ORO	0.155	10	SGA-SGO	0.031	9.5	LSB-NSB	0.072	10
BUL-CAD	0.025	11.5	CHU-EMO	0.148	11	AVA-SSO	0.015	13	ORO-QUE	0.071	11
SGA-SGO	0.025	11.5	KME-OKM	0.147	12	CHE-DEA	0.015	13	COX-IRO	0.071	12
CAD-NOR	0.016	15.5	CSS-PRO	0.142	13	CLI-PRO	0.015	13	CHE-DEA	0.028	13
CHE-DEA	0.016	15.5	LSB-ORO	0.141	14	COX-IRO	0.015	13	NSB-SGA	0.020	14
CSS-PRO	0.016	15.5	CSS-WHA	0.141	15	COX-PRG	0.015	13	SGA-SGO	0.018	15
CSS-WHA	0.016	15.5	ORO-QUE	0.132	16						
KME-OKM	0.016	15.5	ORO-SHE	0.094	17						
NSB-SGA	0.016	15.5	CHU-PRG	0.081	18						
BUL-NBR	0.008	20	SGA-SGO	0.041	19						
CHU-PRG	0.008	20	NSB-SGA	0.039	20						
NOR-SGA	0.008	20	NOR-SGA	0.022	21						

<sup>a</sup> Effectively connected pairs, a measure of short-term network connectivity.

<sup>b</sup> Mean weighted closeness, a measure of long-term network connectivity.



Figure G.1. Prioritization of corridor restoration in the genetic network as ranked by ECP (left panel) and MWC (right panel). Gray lines represent existing corridors. Orange lines represent potentially restorable corridors, with line width inversely proportional to rank (thicker lines are more important restorable corridors for network connectivity). Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.



Figure G.2. Prioritization of corridor restoration in the demographic network as ranked by ECP (left panel) and MWC (right panel). Gray lines represent existing corridors. Orange lines represent potentially restorable corridors, with line width inversely proportional to rank (thicker lines are more important restorable corridors for network connectivity). Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.



Figure G.3. Prioritization of patch restoration in the genetic network as ranked by ECP (left panel) and MWC (right panel). Existing populations are shown with white circles. Orange circles represent potential reintroduction patches, with circle size inversely proportional to ranking (larger circles are more important reintroductions for network connectivity). Solid lines represent existing network edges, dashed lines represent edges associated with patch reintroductions. Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.



Figure G.4. Prioritization of patch restoration in the demographic network as ranked by ECP (left panel) and MWC (right panel). Existing populations are shown with white circles. Orange circles represent potential reintroduction patches, with circle size inversely proportional to ranking (larger circles are more important reintroductions for network connectivity). Solid lines represent existing network edges, dashed lines represent edges associated with reintroductions. Patches are labeled with 3-letter abbreviations; for full patch names, see Table A.1.

# **APPENDIX H: SUPPLEMENTARY MATERIAL FOR CHAPTER 2**

#### **Patch Connectivity Metrics**

We considered four connectivity variables from a previous analysis of bighorn sheep population connectivity in the Mojave Desert (Creech et al., 2014) as potential covariates in the regression of genetic diversity on NDVI. Creech et al. constructed network models of genetic connectivity (the potential for gene flow among populations) and demographic connectivity (the potential for colonization of empty habitat patches) using a geneticbased landscape resistance model (Epps et al. 2007) to estimate the strength of connections between populations in the networks. Bighorn sheep exhibit sex-biased dispersal, with males moving between patches more frequently and over greater distances than females; thus, genetic and demographic connectivity are not equivalent. Genetic connectivity is limited by the maximum effective dispersal distance (ED<sub>MAX</sub>) of males, whereas demographic connectivity is limited by the shorter ED<sub>MAX</sub> of females, as both sexes must disperse in order to colonize an empty habitat patch.

Two network metrics were then calculated, in each network, to characterize the degree to which each patch is connected to other network patches:

- 1. Weighted closeness (WC), which estimates how close a focal patch is to every other patch in a network and accounts for differences in the strength of connections among patches. WC reflects the long-term potential for transfer of genes or individuals to and from the focal patch because it considers all connections, including those with distant patches that would require numerous dispersal steps.
- 2. Effectively connected patches (ECP), which is simply the number of patches connected to a single focal patch along a path (single or multi-step) of effective distance  $\langle ED_{MAX}$ . ECP describes the short-term potential for genetic or demographic connectivity between a focal patch and neighboring patches.

Thus, we used four variables to characterize patch connectivity: demographic network WC, genetic network WC, demographic network ECP, and genetic network ECP. We calculated the correlation between each of these variables and our genetic diversity indices, allelic richness ( $A_r$ ) and expected heterozygosity ( $H_e$ ). Demographic WC was

most highly correlated with both  $A_r$  and  $H_e$  (Table H.1); therefore, we used it as our patch connectivity variable in the analysis of associations between NDVI and genetic diversity.

# References

- Creech T, Epps C, Monello R, Wehausen J (2014) Using network theory to prioritize management in a desert bighorn sheep metapopulation. Landscape Ecology 29(4):605-619
- Epps CW, Wehausen JD, Bleich VC, Torres SG, Brashares JS (2007) Optimizing dispersal and corridor models using landscape genetics. Journal of Applied Ecology 44(4):714-724
| Habitat patch/ abbreviation                                                     | UTM coordinates <sup>1</sup> | Patch area (km <sup>2</sup> ) | # FN<br>samples | # total<br>genotypes | # females<br>genotyped | # males<br>genotyped |
|---------------------------------------------------------------------------------|------------------------------|-------------------------------|-----------------|----------------------|------------------------|----------------------|
| Cady Mountains (CAD)                                                            | 558706 E, 3866694 N          | 280.02                        | 0               | 12                   | 2                      | 10                   |
| Chemehuevi Mountains (CHE)                                                      | 726380 E, 3833368 N          | 250.16                        | 0               | 7                    | 2                      | 5                    |
| Clark Mountains/ S. Spring Range (CSS)                                          | 632064 E, 3942062            | 300.11                        | 0               | 12                   | 7                      | 5                    |
| Clipper Mountains (CLI)                                                         | 646173, E, 3845181 N         | 124.57                        | 0               | 16                   | 7                      | 9                    |
| E. Chocolate Mountains (ECH)                                                    | 714111 E, 3655250 N          | 283.84                        | 0               | 4                    | 2                      | 2                    |
| Eagle Mountains (EMO)                                                           | 629177 E, 3737750 N          | 352.14                        | 0               | 31                   | 11                     | 20                   |
| Granite Mountains (GRA)                                                         | 616799 E, 3853037 N          | 171.10                        | 0               | 21                   | 6                      | 15                   |
| Iron Mountains (IRO)                                                            | 665602 E, 3781324 N          | 97.47                         | 0               | 11                   | 4                      | 7                    |
| Kingston Mountains/ Mesquite Range (KME)                                        | 606266 E, 3956341 N          | 637.53                        | 0               | 5                    | 3                      | 2                    |
| Little San Bernardino Mountains (LSB)                                           | 559311 E, 3761688 N          | 357.54                        | 0               | 12                   | 6                      | 6                    |
| Marble Mountains (MAR)                                                          | 629034 E, 3835474 N          | 112.02                        | 115             | 29                   | 21                     | 8                    |
| Newberry Mountains/ Ord Mountains (NOR)                                         | 527329 E, 3842314 N          | 406.26                        | 0               | 15                   | 12                     | 3                    |
| Old Dad Peak/Kelso Mountains/ Marl Mountains/ Club<br>Peak/ Indian Spring (OKM) | 610459 E, 3888605 N          | 433.17                        | 115             | 37                   | 20                     | 17                   |
| Old Woman Mountains (OWO)                                                       | 666874 E, 3816631 N          | 341.60                        | 0               | 16                   | 15                     | 11                   |
| Orocopia Mountains (ORO)                                                        | 611026 E, 3715465 N          | 323.58                        | 15              | 18                   | 10                     | 8                    |
| Palen Mountains/ Riverside Granite Mountains (PRG)                              | 677337 E, 3748604 N          | 264.53                        | 0               | 10                   | 7                      | 3                    |
| Piute Range/ Castle Peaks/ Castle Mountains (PCC)                               | 674581 E, 3906940 N          | 306.08                        | 0               | 13                   | 10                     | 3                    |
| Providence Mountains (PRO)                                                      | 632555 E, 3866434 N          | 186.12                        | 0               | 20                   | 9                      | 11                   |
| Queen Mountain (QUE)                                                            | 580064 E, 3771509 N          | 136.43                        | 0               | 11                   | 11                     | 0                    |
| Sheephole Mountains (SHE)                                                       | 622644 E, 3785939 N          | 78.89                         | 15              | 0                    | 0                      | 0                    |
| South Bristol Mountains (SBR)                                                   | 614693 E, 3833663 N          | 96.27                         | 15              | 14                   | 7                      | 7                    |
| Turtle Mountains (TUR)                                                          | 700184 E, 3797149 N          | 421.80                        | 0               | 14                   | 11                     | 3                    |
| Woods Mountains/ Hackberry Mountains (WHA)                                      | 657277 E, 3880375 N          | 111.27                        | 0               | 23                   | 5                      | 18                   |

Table H.1. Additional information on location, size, and sampling intensity for habitat patches included in the analysis.

	Correlation with							
Genetic diversity index	Demographic WC	Genetic WC	Demographic ECP	Genetic ECP				
A <sub>r</sub>	0.64	0.62	0.58	0.44				
$H_e$	0.60	0.59	0.55	0.39				

Table H.2. Pearson's correlation coefficient (R) between connectivity metrics and genetic diversity indices.

Table H.3. Pearson correlation coefficient (R) between fecal nitrogen (FN) and each of three summary statistics of the Normalized Difference Vegetation Index (NDVI) in five Mojave Desert bighorn sheep populations. The summary statistic with highest correlation for each population is shown in bold. NDVI summary statistics were log-transformed and FN was exponentiated to linearize the relationship. Median NDVI was used as the NDVI summary statistic in subsequent analyses because it had the highest correlation for the majority of individual populations and for pooled data.

		Correlation with fecal nitrogen				
Population	N	Median NDVI	90 <sup>th</sup> percentile NDVI	Maximum NDVI		
Marble Mountains	115	0.641	0.646	0.649		
Old Dad Peak	115	0.675	0.644	0.641		
Orocopia Mountains	15	0.129	-0.004	0.070		
South Bristol Mountains	15	0.720	0.706	0.545		
Sheephole Mountains	15	0.753	0.768	0.754		
All populations pooled	275	0.511	0.505	0.4899		

Response	Covariates	$P^{\mathrm{a}}$	Pseudo <sup>b</sup> R <sup>2</sup>
$A_r$	median INDVI <sup>c</sup>	0.009	0.69
	(median INDVI) <sup>2</sup>	0.018	
	log(connectivity <sup>d</sup> )	< 0.001	
$A_r$	log(connectivity)	0.001	0.45
A r	median INDVI	0.124	0.35
	$(median INDVI)^2$	0.307	
$H_e$	median INDVI	0.045	0.62
	(median INDVI) <sup>2</sup>	0.074	
	log(connectivity)	0.003	
$H_e$	log(connectivity)	0.002	0.42
$H_e$	median INDVI	0.140	0.32
	(median INDVI) <sup>2</sup>	0.306	

Table H.4. Models of relationship between genetic diversity and long-term NDVI for 22 bighorn sheep populations in the Mojave Desert, with Gaussian spatial correlation structure to account for spatial autocorrelation of genetic diversity among populations.

<sup>a</sup> Significance from *F*-test of  $\beta$ =0 for given covariate

<sup>b</sup> Efron's (1978) pseudo- $R^2$ , a measure of the proportion of variability explained by the model; analogous to traditional  $R^2$  but for generalized least squares

<sup>e</sup> Median of growing-season integrated NDVI values from 2001 through 2011

<sup>d</sup> Demographic weighted closeness (Appendix H), a network-based measure of population connectivity



Figure H.1. Availability of fecal nitrogen data for five bighorn sheep habitat patches in the Mojave Desert: Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE). Rows represent habitat patches and columns represent chronologically ordered months between January 2000 and December 2011. Colored grid cells represent months in which fecal nitrogen was sampled for a given patch. Thicker black vertical lines separate years.







Figure H.3. Comparison of the relationship between FN and untransformed NDVI summary statistics (top row) or log-transformed NDVI summary statistics (bottom row) for the Marble Mountains (MAR) population. Red lines are smooth curves fitted by loess.



Figure H.4. Comparison of the relationship between FN and untransformed NDVI summary statistics (top row) or log-transformed NDVI summary statistics (bottom row) for the Old Dad Peak (OKM) population. Red lines are smooth curves fitted by loess.





time

Figure H.5. Time series (2000-2011) of median NDVI (blue line), 90<sup>th</sup> percentile NDVI (green line), and maximum NDVI (red line) for five habitat patches used in FN analysis: Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE).



Figure H.6. Distribution of NDVI values in one growing season image (26 Feb 2009; shown in green) and one non-growing season image (29 Aug 2009; shown in red) for five habitat patches used in FN analysis: Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE).



Figure H.7. Relationship between fecal nitrogen and Normalized Difference Vegetation Index (NDVI) at the sample level for five populations: Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE) bighorn sheep populations from 2000 through 2011. Regression lines are from the best-fitting model with equal slopes but different intercepts for the patches. Top row of plots shows relationship modeled in linear regression analysis: log-transformed NDVI, FN back-transformed to original scale via exponentiation. Bottom row of plots shows relationship that is most biologically interpretable: NDVI on original scale, FN log-transformed to be linearly related to apparent digestibility.



Figure H.8. Time series of the median Normalized Difference Vegetation Index (NDVI) from 2000 through 2011 for five patches of bighorn sheep habitat in the Mojave Desert that were included in fecal nitrogen analysis: Marble Mountains (MAR), Old Dad Peak (OKM), Orocopia Mountains (ORO), South Bristol Mountains (SBR), and Sheephole Mountains (SHE). Dotted black and gray vertical lines represent January 1 and July 1, respectively, of each year.



Figure H.9. Relationships between IFN or INDVI and peak height or peak width during the 2001 through 2011 growing seasons in the Marble Mountains and Old Dad Peak patches (n=22).



Median INDVI

Figure H.10. Relationship between genetic diversity (expected heterozygosity  $[H_e]$  and allelic richness  $[A_r]$ ) and Normalized Difference Vegetation Index (NDVI) for 22 Mojave Desert populations, after accounting for population connectivity. NDVI is calculated as the median of growing-season integrated NDVI from 2001 through 2011. Plot shows partial residuals from linear model of  $H_e$  or  $A_r$  as a function of median INDVI and log(connectivity).

### **APPENDIX I: GENETIC LABORATORY METHODS**

Genetic samples used in this study were collected during multiple periods and analyzed in three genetics labs: 1) by C. Epps in the Roderick and Palsbol labs at the University of California, Berkeley (samples from 2000-2004; hereafter, "UCB lab"); 2) by the Epps lab at Oregon State University (samples from 2011-2014; hereafter, the "OSU lab"); 3) and by J. Wehausen at White Mountain Research Station in Bishop, CA (samples from 2003-2010; hereafter, the "WMRS lab"). The vast majority of samples consisted of bighorn sheep fecal pellets, but a small number of tissue and blood samples were obtained from live captures, hunter kills, or carcasses found in the field. Because labs used different primer sizes and allele-calling procedures, it was necessary to realign allele sizes for consistency. We accomplished this by genotyping a small subset of samples at each locus used by multiple laboratories and translating all allele sizes to match those used in the OSU laboratory.

We describe the genetic methods used by the OSU lab in detail below. Methods used by the UCB and WMRS labs are similar, and are described in Epps et al. (2005) and Jaeger and Wehausen (2012), respectively. Table I.1 at the end of this appendix gives characteristics of each locus used in this study and the geographic regions and labs in which each locus was used.

### **DNA** extraction

We processed bighorn fecal pellets using the pellet-scraping method detailed in Wehausen et al. (2004) to collect 0.03 g of scrapings from the exterior surface of pellets. We extracted DNA from pellet scrapings using a modified AquaGenomic Stool and Soil protocol (MultiTarget Pharmaceuticals LLC, Colorado Springs, CO). Modifications included the addition of 450  $\mu$ L of AquaGenomic solution to pellet scrapings, the use of 1.0 mm silica/zirconium beads (BioSpec Products Inc., Bartlesville, OK) for cell lysis, and the addition of 12 mAU proteinase K (Qiagen Inc., Valencia, CA) for recovery of mitochondrial DNA. Lastly, we added 150  $\mu$ L of AquaPrecipi solution (MultiTarget Pharmaceuticals) to cell lysate to remove PCR inhibitors present in fecal samples. Tissue samples were extracted using the Qiagen DNeasy blood and tissue kits; we did not quantify DNA concentrations.

#### PCR recipe and cycling conditions

Sixteen dinucleotide microsatellite markers were analyzed in three panels of 4-6 markers (Table I.1). Amplification of most loci was conducted in 10  $\mu$ L reactions consisting of 5x Qiagen Multiplex PCR Master Mix, 10  $\mu$ g of bovine serum albumen, 0.15-0.25  $\mu$ M of each primer and 0.6  $\mu$ L of genomic DNA. Reactions were brought to volume with nuclease-free water. Thermalcycling conditions for the multiplexed loci were as follows: initial denaturation of 15 minutes at 95 °C, followed by 35 cycles of [95 °C for 30 seconds, 60 °C for 90 seconds, 72 °C for 60 seconds], and a final elongation of 30 minutes at 60 °C. For each locus, one primer was fluorescently tagged on the 5' end with NED, PET, VIC (Applied Biosystems, Carlsbad, CA) or 6-FAM (Sigma-Aldrich, St. Louis, MO). Negative and positive controls were included on each genotyping run. PCRs were run on BioRad C1000 and MyCycler thermalcycler machines (Bio-Rad Laboratories Inc., Hercules, CA).

Two markers (BL4 and TGLA387) amplified weakly when pre-PCR multiplexed with other markers; these markers were each run in separate single-locus PCRs and then combined with the rest of the markers from that panel in a post-PCR multiplex. BL4 and TGLA387 were amplified in 10 $\mu$ L reactions consisting of consisting of 1x magnesium-free PCR buffer, 3 mM MgCl<sub>2</sub>, 160  $\mu$ M of each dNTP, 10  $\mu$ g bovine serum albumin, 0.35  $\mu$ M of each primer, 0.7 units of Hot Start *Taq* polymerase (Apex Bioresearch Products) and 0.6 $\mu$ L of genomic DNA, and then brought to volume with nuclease-free water. Thermalcycling conditions were as follows: initial denaturation of 15 minutes at 95 °C, followed by 40 cycles of [95 °C for 30 seconds, 45 seconds at 60 °C (BL4) or 52 °C (TGLA387), and 72 °C for 30 seconds], with a final elongation step of five minutes at 72 °C.

## Typing

Each sample was amplified in three replicate PCRs for the six markers in panel 1 (Table I.1). We generated consensus genotypes across all three replicates: for a homozygous genotype to be considered verified, the allele had to be typed in three separate replicates. To confirm a heterozygous genotype, each allele had to be observed at least twice. Samples with incomplete or discrepant data were rerun in an additional 3-6 replicates.

Any sample that consistently showed more than 2 alleles at a single locus was considered contaminated and removed.

Amplification products were visualized on a 2% agarose gel prestained with GelRed (Biotium Inc., Hayward, CA). Products were diluted accordingly, ethanol-precipitated to remove salts, and submitted for fragment size analysis on the ABI DNA 3730 DNA analyzer (Applied Biosystems) at the Oregon State University Center for Genome Research and Biocomputing (Corvallis, OR). We used GeneScan 500 LIZ dye size standard (Applied Biosystems), and called allele sizes in GeneMapper v.4.1 (Applied Biosystems).

# **Identifying duplicates**

We grouped samples into major regions comprising all populations within or near each national park unit (e.g., Death Valley, Glen Canyon, Grand Canyon, etc.) before identifying duplicates. In some cases, major genetic divisions with different allele frequencies existed within a region (e.g., populations on either side of the Colorado River in Grand Canyon), so we analyzed these subregions independently. We used program CERVUS version 3.0.3 (Kalinowski et al. 2007) to calculate the allele frequencies and probability of identity (P<sub>ID</sub>) for each region (or subregion) using the six markers in Panel 1. Since missing data most frequently occurred for locus TGLA387 in any sample, we recalculated the  $P_{ID}$  using only the other five markers in Panel 1. We then searched for duplicate individuals within a region, using the minimum number of loci required to have a  $P_{ID}$  for unrelated individuals of <0.01 (because most regions were generally estimated to have <100 sampled individuals), and a P<sub>ID</sub> for siblings of <0.05. We ran additional searches for duplicates using decreased stringency (i.e., allowed fuzzy matching) until CERVUS began returning matches that were unlikely due to sampling location (e.g., putative duplicates sampled hundreds of kilometers apart) or the inability to explain mismatches with allelic dropout (e.g., heterozygotes with different alleles). When duplicate samples were discovered, we removed all but one from further analyses. Samples that had too much missing data were retained in the data set and run with additional markers until we could verify whether or not they were unique.

We then ran putative unique genotypes for the remaining two panels (10 loci) and reran the CERVUS analyses using all 16 markers to recalculate  $P_{ID}$  and the minimum

number of loci to identify matches. In this manner, we removed additional duplicates that did not amplify at enough markers in Panel 1 to be excluded. Finally, samples with fewer than 5 loci successfully typed were removed from the data set. The mean number of loci successfully typed per sample in the final dataset was 15.4, with at least 13 loci successfully typed for 95 percent of samples.

# Error rates and equilibrium tests

We used GIMLET version 1.3.3 (Valière 2002) to estimate genotyping error rates (both false allele occurrence rate and allelic dropout rate) for a subset of regions with varying sample sizes (Glen Canyon, Death Valley, Capitol Reef, Utah BLM lands). False allele occurrence rate was zero for all regions tested, and allelic dropout rate averaged 4.1 percent across loci and regions.

We used GENEPOP version 4.2 (Raymond and Rousset 1995) to test for deviations from linkage equilibrium (LE) and Hardy-Weinberg equilibrium (HWE) in each sampled population within each region and corrected for multiple comparisons. We observed deviations from HWE or LE in a number of populations; however, no locus (for HWE) or pair of loci (for LE) was consistently out of equilibrium across populations, suggesting that these deviations most likely resulted from population substructure rather than non-neutral loci or non-independent loci. We therefore retained all loci in subsequent analyses.

# References

- Buchanan FC, Crawford AM (1992a) Ovine dinucleotide repeat polymorphism at the MAF209 locus. Animal Genetics 23(2):183
- Buchanan FC, Crawford AM (1992b) Ovine dinucleotide repeat polymorphism at the MAF33 locus. Animal Genetics 23(2):186.
- Buchanan FC, Crawford AM (1993) Ovine microsatellites at the OarFCB11, OarFCB128, OarFCB193, OarFCB266, and OarFCB304 loci. Animal Genetics 24(2):145.
- Buchanan FC, Swarbrick PA, Crawford AM (1991) Ovine dinucleotide repeat polymorphism at the MAF65 locus. Animal Genetics 23(S1):85
- Buchanan FC, Swarbrick PA, Crawford AM (1992) Ovine dinucleotide repeat polymorphism at the MAF48 locus. Animal Genetics 22(4):379-380
- Crawford AM, Dodds KG, Ede AJ, Pierson CA, Montgomery GW, Garmonsway HG, Beattie AE, Davies K, Maddox JF, Kappes SW, Stone RT, Nguyen TC, Penty FM, Lord EA, Broom JA, Buitkamp J, Schwaiger W, Epplen JT, Matthew P, Matthews ME, Hulme DJ, Beh KJ, McGraw RA, Beattie CW (1995) An autosomal genetic linkage map of the sheep genome. Genetics 140(2):703-724

- Ede AJ, Pierson CA, Henry H, Crawford AM (1994) Ovine microsatellites at the OarAE64, OarHH22, OarHH56, OarHH62, and OarVH4 loci. Animal Genetics 25(1):51-52
- Ede AJ, Pierson CA, Crawford AM (1995) Ovine microsatellites at the OarCP9, OarCP16, OarCP20, OarCP21, OarCP23, and OarCP26 loci. Animal Genetics 26(2):129-130
- Epps CW, Palsbøll PJ, Wehausen JD, Roderick GK, Ramey RR, McCullough DR (2005) Highways block gene flow and cause a rapid decline in genetic diversity of desert bighorn sheep. Ecology Letters 8(10):1029-1038
- Georges M, Massey J (1992) Polymorphic DNA markers in Bovidae. In: WO Publication No. 92/13120. World Intellectual Property Organisation, Geneva
- Henry HM, Penty JM, Pierson CA, Crawford AM (1993) Ovine microsatellites at the OarHH35, OarHH41, OarHH44, OarHH47 and OarHH64 loci. Animal Genetics 24(3):222
- Jaeger JR, Wehausen JD (2012) Development of a habitat management plan to maintain viability of the desert bighorn sheep population in the River Mountains, Nevada: analysis of mitochondrial DNA diversity and connectivity. Final Report to the National Park Service, Lake Mead National Recreation Area. University of Nevada, Las Vegas
- Kalinowski ST, Taper ML, Marshall TC (2007) Revising how the computer program Cervus accommodates genotyping error increases success in paternity assignment. Molecular Ecology 16(5):1099-1106
- Pentry JM, Henry HM, Ede AJ, Crawford AM (1993) Ovine microsatellites at the OarAE16, OarAE54, OarAE57, OarAE119, and OarAE129 loci. Animal Genetics 24(3):219
- Raymond M, Rousset F (1995) GENEPOP (version 1.2): population genetics software for exact tests and ecumenicism. Journal of Heredity 86(3):248-249
- Smith TP, Lopez-Corrales N, Grosz MD, Beattie CW, and Kappes SM (1997) Anchoring of bovine chromosomes 4, 6, 7, 10, and 14 linkage group telomeric ends via FISH analysis of lambda clones. Mammalian Genome 8(5):333-336
- Steffen P, Eggen A, Stranzinger G, Fries R, Dietz A, Womack J (1993) Isolation and mapping of polymorphic microsatellites in cattle. Animal Genetics 24(2):121-124
- Swarbrick P, Buchanan F, Crawford A (1991) Ovine dinucleotide repeat polymorphism at the MAF35 locus. Animal Genetics 22(4):369-370
- Valière, N (2002) GIMLET: a computer program for analysing genetic individual identification data. Molecular Ecology Notes 2(3):377-379
- Wehausen JD, Ramey RR, Epps CW (2004) Experiments in DNA extraction and PCR amplification from bighorn sheep feces: the importance of DNA extraction method. Journal of Heredity 95(6):503-509

	No. alleles	Size range			
Locus	observed	(base pairs)	Regions <sup>1</sup>	Labs <sup>2</sup>	Reference
AE129	11	167-189	AR, CR, CY, DV, GL, GR, LM, MV <sup>5</sup> , UT, ZI	OSU, WMRS	Pentry et al. 1993
AE16	9	82-98	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Pentry et al. 1993
BL4	5	156-164	AR, CR, CY, DV, GL, GR, MV <sup>3</sup> , UT, ZI	OSU, WMRS	Smith et al. 1997
CP20	11	76-96	$MV^4$	UCB	Ede et al. 1995
D5S2	9	202-220	$MV^4$	UCB	Steffen et al. 1993
FCB11	5	121-131	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan and Crawford 1993
FCB128	2	113-115	$\mathrm{DV}^6,\mathrm{MV}^4$	UCB, WMRS	Buchanan and Crawford 1993
FCB193	8	105-119	AR, CR, CY, DV, GL, GR, LM, MV <sup>5</sup> , UT, ZI	OS, WMRS	Buchanan and Crawford 1993
FCB266	8	89-105	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan and Crawford 1993
FCB304	5	138-150	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan and Crawford 1993
HH47	11	129-151	$MV^4$ , $DV^6$	UCB, WMRS	Henry et al. 1993
HH62	16	100-130	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Ede et al. 1994
JMP29	12	121-145	AR, CR, CY, DV, GL, GR, LM, MV <sup>5</sup> , UT, ZI	OSU, WMRS	Crawford et al. 1995
MAF209	8	110-124	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan and Crawford 1992a
MAF33	7	120-132	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan and Crawford 1992b
MAF36	9	87-105	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Swarbrick et al. 1991
MAF48	6	120-130	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan et al. 1992
MAF65	15	112-148	AR, CR, CY, DV, GL, GR, LM, MV, UT, ZI	OSU, WMRS, UCB	Buchanan et al. 1991
TCRBV62	8	167-181	AR, CR, CY, DV, GL, GR, LM, MV <sup>5</sup> , UT, ZI	OSU, WMRS	Crawford et al. 1995
TGLA387	7	141-153	AR, CR, CY, DV <sup>7</sup> , GL, GR, MV <sup>3</sup> , UT, ZI	OSU	Georges and Massey 1992

Table I.1. Microsatellite locus information.

<sup>1</sup>Samples from some regions were genotyped at only a subset of loci. AR=Arches, DV=Death Valley, CR=Capitol Reef, CY=Canyonlands, GL=Glen Canyon, GR=Grand CanyonLM=Lake Mead, MV=Mojave (includes Mojave NP and Joshua Tree NP), UT=southeast Utah BLM lands, ZI=Zion.

 $^{2}$ Labs used different subsets of the 20 loci in this study. OSU = Oregon State University; UCB = University of California, Berkeley; WMRS = White Mountain Research Station.

<sup>3</sup>MV region was sampled during multiple periods; ~5% of MV samples were genotyped at this locus at the OSU lab; remaining samples were not genotyped at this locus.

<sup>4</sup>MV region was sampled during multiple periods; ~80% of MV samples were genotyped at this locus at the UCB lab; remaining samples were not genotyped at this locus.

<sup>5</sup>MV region was sampled during multiple periods; ~20% of MV samples were genotyped at this locus at the OSU and WMRS labs; remaining samples were not genotyped at this locus.

<sup>6</sup>DV region was sampled during multiple periods; only earlier period DV samples analyzed in the WMRS lab were genotyped at this locus.

<sup>7</sup>DV region was sampled during multiple periods; only later period DV samples analyzed in the OSU lab were genotyped at this locus.

# **APPENDIX J: GEOSPATIAL DATA FOR CHAPTER 3**

Variable	Data description	Original spatial resolution	Source
Slope	Slope in degrees, derived from digital elevation model using ArcGIS 10.1	1/3 arcsecond (~10 m)	DEM from National Elevation Dataset (http://ned.usgs.gov/)
NDVI	Average of annual total integrated NDVI values during 2000-2013	250 m	USGS Eros Center (http://phenology.cr.u sgs.gov/)
Distance to water	Distance to the nearest permanent surface water source	Vector data	National Hydrography Dataset; National Park Service
Water barriers	Water features believed to act as strong barriers to bighorn sheep	Vector data	National Hydrography Dataset (http://nhd.usgs.gov/)
Anthropogenic development	Converted (versus natural) cover types	30 m	2011 National Land Cover Database
Major roads	Divided, fenced highways	Vector data	U.S. Census (www.census.gov)
Forested areas	Evergreen, deciduous, and mixed forest cover types	100 m	2011 National Land Cover Database

Table J.1. Geospatial data sources for landscape variables.

#### **APPENDIX K: LANDSCAPE RESISTANCE MODELS FOR CHAPTER 3**

We used three equations to describe the relationships between continuous landscape variables and resistance, where resistance varies between 1 and a user-defined maximum resistance value. Equation K.1 describes possible resistance curves when resistance values and landscape variable values are expected to be positively related:

$$r = \frac{x^{\alpha}}{x_{max}^{\alpha}} * (r_{max} - 1) + 1$$
 (Eqn. K.1)

where *r* is resistance,  $r_{max}$  is the maximum resistance value, *x* is the value of the landscape variable,  $x_{max}$  is the maximum landscape variable value observed within the three study regions, and  $\alpha$  is an exponent that controls the shape of the relationship. For landscape variables expected to be negatively related to resistance, we used Eqn. K.2:

$$r = r_{max} - \frac{x^{\alpha}}{x_{max}^{\alpha}} * (r_{max} - 1)$$
 (Eqn. K.2)

Depending on the value of  $\alpha$ , these equations specify relationships that can be either concave-up or concave-down (Fig. K.1). When  $\alpha = 1$ , the relationships are linear.

Some landscape variables could exhibit lowest resistance at an intermediate value; for instance, very shallow slopes may expose bighorn sheep to predation and very steep slopes may be difficult to negotiate, while intermediate slopes might offer the least resistance. Following Castillo et al. (2014), we modeled these relations using an inverse Gaussian function:

$$r = r_{max} - (r_{max} - 1) * e^{(-\frac{(x - x_{opt})^2}{2x_{sd}^2})}$$
 (Eqn. K.3)

where  $r_{max}$  is the maximum resistance value, x is the value of the landscape variable,  $x_{opt}$  is the optimal (i.e., lowest resistance) value of the landscape variable, and  $x_{sd}$  is the standard deviation of the normal curve (Fig. K.2).



Figure K.1. Monotonic relationships resulting from Eqn. K.1 (left panel) and Eqn. K.2 (right panel) for a range of  $\alpha$  values and a hypothetical landscape variable with  $x_{max} = 100$  and  $r_{max} = 100$ .



Figure K.2. Gaussian relationships resulting from Eqn. K.3 for a range of  $x_{sd}$  values (left panel) or  $x_{opt}$  values (right panel) and a hypothetical landscape variable with  $x_{max} = 100$  and  $r_{max} = 100$ .

Table K.1. Alternative resistance curves for continuous landscape variables. All possible combinations of parameter values for each variable were used as candidate univariate resistance surfaces in all three regions, with two exceptions: 1) major roads resistance surfaces were not tested for DEVA or GRCA because no major roads exist within these regions; and 2) water barrier resistance features were not tested within DEVA because no water barriers exist within the DEVA region.

Variable	Curve description	Parameters
	Linear	$R_{max} = 10; 50; 100   \alpha = 1$
	Concave up	$R_{max} = 10; 50; 100   \alpha = 0.25$
	Concave down	$R_{max} = 10; 50; 100   \alpha = 4$
	Gaussian	$R_{max} = 10; 50; 100   x_{opt} = 30;$
Slope		40; 50   $x_{sd} = 20$ ; 40; 60
	Break point	ratio = 5; 10; 20   lower break
		= 10; 15; 20   upper break =
		45; 55; 65
	Linear	$R_{max} = 10; 50; 100   \alpha = 1$
D 1	Concave up (weak)	$R_{max} = 10; 50; 100   \alpha = 0.25$
Ruggedness	Concave down (strong)	$R_{max} = 10; 50; 100   \alpha = 4$
	Linear	$R_{max} = 10.50.100   \alpha = 1$
	Concave up (weak)	$R_{max} = 10; 50; 100   \alpha = 0.25$
NDVI	Concave down (strong)	$R_{max} = 10; 50; 100   \alpha = 0.25$ $R_{max} = 10; 50; 100   \alpha = 4$
	concuve down (strong)	$R_{\text{max}} = 10, 50, 100  \text{w}$
Distance to	Linear	$R_{max} = 10; 50; 100   \alpha = 1$
Distance to	Concave up (weak)	$R_{max} = 10; 50; 100   \alpha = 4$
water	Concave down (strong)	$R_{max} = 10; 50; 100   \alpha = 0.25$

Variable	Resistance ratios												
	5	10	25	50	100	250	500	1,000	5,000	10,000	50,000	100,000	1,000,000
Anthropogenic development	~	~	~	~	~	✓	~	✓	~	✓			
Major roads		~		✓	~		~	$\checkmark$	~	✓	✓	✓	
Forested areas	~	✓	~	✓	~	~	~	$\checkmark$					
Water barriers		~		$\checkmark$	~		~	$\checkmark$	~	$\checkmark$	$\checkmark$	$\checkmark$	$\checkmark$

Table K.2. Alternative resistance ratios for categorical landscape variables.

# **APPENDIX L: GENETIC STUCTURE ANALYSIS**



Figure L.1. Likelihood estimate (mean  $\pm$  standard deviation from 10 replicates) for each value of *K* from STRUCTURE analysis for 62 desert bighorn sheep populations.



Figure L.2. Rate of change in the likelihood function ( $\Delta K$  from Evanno et al. 2005) from STRUCTURE analysis for 62 desert bighorn sheep populations.



Figure L.3. Individual cluster assignment probabilities from STRUCTURE analysis for 62 desert bighorn sheep populations. Each vertical bar represents an individual, and colors show proportional assignment to each cluster. Individuals are grouped by population - see Table 1 for population abbreviations. A) Results for K=2. B) Results for K=4. Cluster colors correspond to those in Fig. 2A and 2B, respectively.

## **APPENDIX M: LANDSCAPE RESISTANCE MODEL FOR CHAPTER 4**

We estimated the area within dispersal range of each habitat patch using a landscape resistance model derived from the results of Chapter 3. In that chapter, we used a subset of the genetic data included in this study to independently optimize landscape resistance models for three regions: Death Valley (DEVA), Southern Mojave Desert (MOJA), and Grand Canyon (GRCA). We tested for the effects of seven landscape variables: slope, Normalized Difference Vegetation Index (NDVI), anthropogenic development, major roads, distance to water, forested areas, and water barriers. The analysis resulted in similar but not identical models for the three regions.

We used these results to develop a composite resistance model to apply across the entire study area, including only those landscape variables that exhibited a strong influence on gene flow in each region (assuming the landscape variable was present in the region; for instance, no major roads were present in DEVA). Variables that met this criterion were slope, major roads, and water barriers. Major roads and water barriers were 5,000 times more resistant to movement than terrain that did not include either of these features. The effect of slope was modeled using a Gaussian function in which resistance was lowest at an intermediate slope value and increased at higher or lower slopes. Some parameters associated with this Gaussian model (maximum resistance value, optimal slope value) varied among regions.

Our composite model included additive effects of each of these three variables on landscape resistance. For slope, we used the modal value (or the median value if no modal value existed) for model parameters that varied among the three regions: optimal slope =50 degrees; standard deviation of Gaussian curve = 20 degrees; maximum resistance 50 times higher for most-resistance slope value than for optimal slope value.

# APPENDIX N: RELATIONSHIP BETWEEN GENETIC DIVERSITY AND CONNECTIVITY

Genetic diversity and landscape connectivity are expected to be strongly correlated in most natural systems because connectivity allows for gene flow among populations that helps to maintain genetic diversity. However, in our study system, the relationship between genetic diversity and connectivity is quite weak. To demonstrate this, we fit linear models of genetic diversity (measured as allelic richness or expected heterozygosity) verus connectivity (measured as the area of occupied habitat within a maximum dispersal threshold) for the 62 bighorn sheep populations included in our study. Relationships were non-significant ( $P \ge 0.12$ ) for both genetic diversity metrics. The scatterplots in Figure N.1 below further illustrates the weak relationship between genetic diversity and connectivity in our study area.



Figure N.1. Relationship between genetic diversity and connectivity of 62 desert bighorn sheep populations. Genetic diversity is measured as allelic richness (top panel) or expected heterozygosity (bottom panel). Connectivity is measured as the area of occupied habitat within a maximum dispersal range. Black line is best-fit line from linear regression of each genetic diversity metric on connectivity