DOES MIGRATION MATTER?
CAUSES AND CONSEQUENCES OF MIGRATORY BEHAVIOR IN SIERRA NEVADA BIGHORN SHEEP

By
DEREK BENJAMIN SPITZ
B. A. Biology, University of Chicago, Chicago, IL, 2009

Dissertation
presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Fish and Wildlife Biology

The University of Montana
Missoula, MT

December 2015

Approved by:

Sandy Ross, Associate Dean of The Graduate School
Graduate School

Mark Hebblewhite, Chair
Dept. of Ecosystem and Conservation Science, Wildlife Biology Program,
University of Montana

Winsor H. Lowe
Dept. of Ecosystem and Conservation Science, Wildlife Biology Program,
University of Montana

L. Scott Mills
Dept. of Forestry and Environmental Resources, College of Natural Resources,
North Carolina State University

Michael S. Mitchell
Dept. of Ecosystem and Conservation Science, Wildlife Biology Program,
University of Montana

Thomas R. Stephenson
California Department of Fish and Game

Spitz, Derek, Ph.D, Fall 2015 *Fish and Wildlife Biology*

Does migration matter? Causes and consequences of migration in Sierra Nevada bighorn sheep

Chair: Mark Hebblewhite

Despite their potential conservation importance, the demographic implications of migratory behavior remain poorly understood. Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; hereafter “Sierra bighorn”) are federally-endangered and partially migratory. In summer, Sierra bighorn share high-elevation summer ranges, but in winter some individuals migrate to lower elevation for winter while others remain resident at high-elevation. Lower elevations have better forage in winter, but these areas also carry an increased risk of predation from Sierra bighorn's primary predator, the cougar (*Puma concolor*). We should therefore expect differences in winter conditions to result in demographic differences between migrants and residents.

First, I developed new software tools in an open-source R package ‘migrateR’ for classifying migratory behavior, including novel techniques for identifying altitudinal migration. Applying these tools to Sierra bighorn showed that migratory behavior in this taxon is extremely flexible in both status (migrant v. resident) and tactics (e.g. timing, duration of movements), with individuals frequently switching migratory status between years.

I tested for status-specific differences in winter resource use and selection by migrants and residents using resource selection functions across three scales. Migrants and residents showed scale-specific differences in resource selection offering contrasting solutions to a forage-predation tradeoff. Residents avoided predation risk at the coarsest scale, but focused on forage in fine-scale selection, whereas migrants selected for forage at the coarsest spatial scale and focused on avoided predation risk at finer scales. This pattern of selection resulted in migrants gaining better access to forage. The amount of migrant habitat predicted differences in the prevalence of migration across eight populations.

Lastly, I tested causes and consequences of migratory behavior in Sierra bighorn. Migratory propensity increased with winter severity. Individuals that were still lactating in fall were highly likely to migrate, but the strength of this effect declined with body mass. I failed to find an effect of winter elevation on adult female survival. Finally, Sierra bighorn were more likely to be observed with a lamb following residency than following migration. These results suggest that where residency is viable, residents make greater per-capita contributions to population growth than do migrants.

ACKNOWLEDGEMENTS

Fully enumerating the gratitude I feel for the past four and a half years borders on impossibility. The years have been full. Above all, I am indebted to Dr. Mark Hebblewhite for his generosity and dedication as an advisor and mentor. Mark consistently showed great patience in allowing me the freedom to make the mistakes I needed while showing tremendous kindness in warning me against following certain rabbit holes too far down. I am similarly indebted to Dr. Tom Stephenson for his continuing guidance and encouragement since entering the wildlife field. I blame Dr. Kevin Monteith for the discovery of a field that I love.

This research would be impossible without the tenacious field efforts of the California field team, which has been built by the epic effort of Todd Calfee, Alex Few, Kelsey Ellis, Jonathan Fusaro, Brian Hatfield, Armin Howell, Dennis Jenson, Kathleen Knox, Julia Runcie, and Ryan Spaulding. Heather Johnson was the first to train me for work with bighorn and to suggest I consider returning to school. Lacey Greene first introduced me to the analytical challenges of graduate research. Dave German gave me an invaluable early lesson on the folly of technophobia. Heather Johnson was the first to train me in observing bighorn and to suggest I consider returning to school. I thank John Wehausen for his love of observation, enthusiasm for the scientific process and eagerness to share knowledge hard-earned.

I cannot express the extent to which my intellectual growth is indebted to fellow graduate students, particularly members of the Heblab past and present: Sonja Christensen, Nick DeCesare, Dan Eacker, Scott Eggeman, Josh Goldberg, Lacey Greene, Nicole Hupp, Mark Hurley, Andrew Jakes, Clayton Miller, Robin Steenweg, Tshering Tempa and especially Wibke Peters. Joe Smith and Mike LeMoine also provided collaboration and humor at several key junctures. There are many others at the university deserving special thanks, especially my committee members, Drs. Winsor Lowe, L. Scott Mills and Michael Mitchell, who provided valuable feedback on much of what follows. Josh Nowak entertained questions of varying scope with kindness and characteristic patience. Catherine Redfern and Jim Adams made the otherwise onerous tasks of hiring and grant management a true pleasure. Like many before me, I've depended on Jeanne Franz's guidance. As we all know, she is an unstoppable force of helpfulness.

With time I have come to increasingly appreciate the profound influence of my friends and family. I thank my father for introducing me to the mountains and showing me that you can follow your recreation into a fulfilling career and thank my mother for helping me learn that a compass is only useful if you don't know where you're going. I am also most grateful for the acceptance and support of my new family Sharon, Frank and Hannah as well as my wife Emma. Emma's irrepressible kindness, curiosity and laughter have become one of my life's few constants. I cannot appreciate enough the sense of stability these landmarks provide. Finally I thank the communities of friends who have made me feel at home in Bishop, Fort Collins and Missoula.

Financial support for this research was provided by the California Department of Fish and Wildlife.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1.

INTRODUCTION AND OVERVIEW

What is the goal of conservation? Recognition of the pervasiveness of anthropogenic disturbances is forcing a reevaluation of this challenging question (Kareiva and Marvier 2012; Doak et al. 2014). Animal migration serves as an interesting case study, making a case for the expansion of our understanding of conservation beyond the traditional goals of protecting species and ecosystems. Migration is a well-known and often dramatic phenomenon found across a wide array of environments and taxa. Ecologically, migrants play an important role as trophic links, ferrying resources between ecosystems (Bauer and Hoye 2014). Migratory species can also have huge economic value (Gordon et al. 2004; Milner-Gulland et al. 2011). Unfortunately, many migratory species share another similarity; they currently face global declines that threaten their persistence (Bolger et al. 2008; Wilcove and Wikelski 2008; Robinson et al. 2009). The dynamics driving these declines, however, remain poorly understood. One of the factors that make these dynamics difficult to unravel is that most migratory populations also include residents who forgo migration, a phenomenon known as partial migration (Chapman et al. 2011). Migrants and resident behavior is itself a form of resource selection that results in different individuals experiencing different conditions through part of the year and may consequently be expected to show demographic differences (e.g. Adriaensen and Dhondt 1990). In many taxa, migrants are less successful than migrants (Gillis et al. 2008;

Grayson et al. 2011; Skov et al. 2011). Where migration is a less successful strategy, this presents a conundrum to those seeking to manage or conserve these populations: even if we succeed in protecting a species or population, it may still be possible to lose migratory behavior (Berger 2004; Wilcove and Wikelski 2008). Preserving migration and the species and ecosystems it supports may thus require us to focus on the conservation of a behavior rather than a species. To conserve migration we must first develop a fuller understanding of the causes and consequences of migratory behavior (Bolger et al. 2008).

Theory provides two competing explanations for the evolution and persistence of partially migratory populations, each suggesting a different direction for the conservation and management of partially migratory populations (Lundberg 1987, 1988; Kaitala et al. 1993). These explanations hinge on the level of flexibility present in migratory behavior. First, if migratory strategy is fixed at the individual level, the demographic payoff of migration and residency must, on average, balance for both strategies to persist through time. One consequence of this is that migrants and residents can be treated and studied as two separate "populations" with independent demography (Kaitala et al. 1993). Thus if migratory strategy is fixed at the individual level, the dynamics of a partially migratory population can be easily evaluated by comparing the growth rate of migrant and resident populations. A further consequence, however, is that any loss of migratory behavior is likely to be permanent. Alternately, partial migration may result from a conditional strategy, in which individuals can switch between migration and residency in different years. Under a conditional strategy, any loss of migratory behavior is likely to be temporary, but drivers of population demography are more difficult to identify. As a conditional strategy, migration does not need to have the same demographic payoff as residency. Furthermore, in these systems demography depends not only on the demographic performance of migrants and residents, but also the drivers and frequency of strategy switching at the individual level, (see, e.g., Gillis et al. 2008) thus requiring a more detailed and holistic approach to testing the drivers of population demography. Numerous studies of condition-dependent migration in fish, birds and amphibians have shown migration to be an inferior strategy in which migrants “make the best of a bad situation” (Gillis et al. 2008; Grayson et al. 2011; Skov et al. 2011). Evidence from mammals, however, is far less clear. Ungulates have often been assumed to exercise fixed strategies, but recent evidence suggests that many members of this taxon are in fact conditional migrants (e.g. Eggeman 2012; Morrison and Bolger 2012; White et al. 2013). The causes and demographic consequences of these behaviors remain poorly understood.

North America's rarest ungulate, the federally-endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*, Sierra bighorn hereafter), is a partially-migratory alpine specialist (U. S. Fish and Wildlife Service 2007). Sierra bighorn were placed on the federal endangered species list in 1999 and California Department of Fish and Wildlife has been the lead agency managing the species for recovery (U. S. Fish and Wildlife Service 2007). The species decline began over a century earlier following European colonization of California's Sierra Nevada mountains beginning in the mid nineteenth century. Sierra bighorn were nearly extirpated before receiving scientific scrutiny, and consequently the species' former distribution remains poorly understood (U. S. Fish and Wildlife Service 2007). Currently Sierra bighorn persist in a number of demographically distinct sub-populations that are mostly stable or slowly growing (Johnson et al. 2010). This species is slow to naturally recolonize unoccupied portions of it's range and so recent conservation efforts have focused on expanding the distribution of Sierra bighorn through manual reintroductions (U. S. Fish and Wildlife Service 2007). Managers, however, largely lack the quantitative tools needed to meaningfully inform the choice of reintroduction sites. Migration in Sierra bighorn is altitudinal. Sierra bighorn share high-elevation summer ranges in the Sierra Nevada mountains, California, USA, but in winter some individuals retreat to lower elevations for winter, while others remain on high-elevation ranges as year-round residents. Following observation of other migratory ungulates, migrant Sierra sheep are hypothesized to benefit from increased access to forage (Fryxell and Sinclair 1988; Albon and Langvatn 1992; Hebblewhite et al. 2008). Migrant sheep, however, are expected to pay dearly for this benefit with increased predation risk resulting in lower adult survival. In a classic example of apparent competition, migration leads Sierra sheep to overlap with the winter ranges of large mule deer (*Odocoileus* hemionus) herds that support a superabundance of Sierra bighorn's primary predator, the cougar (*Puma concolor*; Johnson et al. 2012). Cougars are expected to spend the winter hunting at lower elevations and hence pose comparatively little risk to residents, whose high-elevation ranges keep them more isolated.

In the chapters that follow I present a series of analyses building toward the larger goal of understanding the causes and consequences of partial migration in Sierra bighorn. First, I develop new software for the classification and quantification of migratory behavior. This software package, “migrateR”, written for the open source Program R (R

Core Team 2014) automates existing model-driven classification techniques (i.e. Bunnefeld et al. 2011) to classify animal movement as migratory resident or other behavior (disperal, etc.) based on global positioning system (GPS) radiotelemetry data, and includes improvements designed to address previously noted limitations of this approach. These improvements include: 1) a re-parameterization that provides a means of reducing the bias against classifying resident behavior; 2) calculation of modified movement metric that reduces sensitivity to choice of start date; and 3) a novel expansions of methods suitable for the classification of altitudinal migration. I illustrate the software with data from Sierra bighorn and elk (*Cervus elaphus*) from Canada's Rocky Mountains (Chapter 2). Despite my focus here on ungulates, this R package will be useful for analysis of all migratory species spatial location data.

Second, I applied the methodological advances I developed in migrateR to Sierra bighorn to classify individual behavior by year as migrant or resident. In comparing migratory strategy for marked individuals through time, I found this taxon to have one of the highest rates of strategy switching so far recorded in any ungulate, and thus concluded that here migration represents a conditional strategy. I also used model-driven classification methods to characterize the timing and duration of migratory movements as well as the prevalence of migration among 8 sub-populations. (Chapter 3). The evidence I report for flexibility and conditionality in migratory behavior leads, in the chapters that remain, to my focus on addressing causes and consequences of this migratory flexibility.

Next, I quantified strategy-specific differences in winter resource use and selection by Sierra bighorn ewes. To test differences in selection I built a scale-independent resource selection function (DeCesare et al. 2012), which integrated selection across three scales: within species range, within population range and within home range. In a classic forage-predation tradeoff, migrants and residents showed contrasting scale-specific patterns of selection. Residents avoided predation risk at coarse scales and focused on selecting forage at finer scales whereas migrants displayed the opposite pattern with forage driving selection at coarse scales, but avoidance of predation risk dominating finer-scale selection. Integration of strategy-specific selection across scales revealed that this scale-specific selection for forage and safety was countervailing leading to similar patterns of spatial predictions for migrants and residents. Ultimately, use did differ between the strategies with migrants gaining increased access to forage as hypothesized (Chapter 4).

Fourth, I tested potential causes and consequences of Sierra bighorn migration. I found that migratory propensity increased with winter severity but that this effect decreased with body mass such that smaller individuals were most sensitive to winter severity and the largest animals in our study were nearly insensitive to this cue. I also found that migratory strategy was important to explaining a reproductive correlate, the probability of observing an ewe with a lamb-at-heel during summer. Ewes were more likely to be observed with a lamb following residency rather than migration. Combined with the lower adult survival expected of migrants as a consequence of predation (Johnson et al. 2012) the resident strategy thus appears more successful (Chapter 5).

Inferior demographic performance by migrants has often been interpreted as evidence that migration is a losing strategy in which individuals are forced to “make the best of a bad situation” (Gillis et al. 2008; Grayson et al. 2011; Skov et al. 2011). Our results, however, do not support this interpretation. In several isolated sub-populations we only observed the migrant strategy (Chapter 3). Past work on these sub-populations shows that they can support large populations and that they've acted as source populations responsible for seeding near by recolonizations (Johnson et al. 2010; California Department of Fish and Wildlife, unpublished data). Hence migration is not necessarily a losing strategy, but a conditional strategy whose success depends on context. Migration complements residency allowing Sierra bighorn to persist in areas that lack the resources required to support residency (Fryxell et al. 1988). In harsh landscapes migration may thus play an important role in maintaining genetic and demographic links among metapopulations (Pulliam 2000; Johnson et al. 2011). Based on the demographic advantages of residency, we recommend that reintroduction efforts for this species focus on identifying high-elevation ranges capable of supporting residency.

Dissertation Format

Footnotes at the beginning of the chapters that follow indicate where I have formatted my work for publication in specific peer-reviewed scientific journals. As each of these chapters reflects the contributions of several important collaborators, I employ the collective “we” throughout the remainder of this dissertation.

References

ADRIAENSEN, F. AND A. A. DHONDT. 1990. Population-Dynamics and Partial Migration of the European Robin (Erithacus rubecula) in Different Habitats. Journal of Animal Ecology 59:1077–1090.

ALBON, S. AND R. LANGVATN. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502–513.

BAUER, S. AND B. J. HOYE. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science (New York, N.Y.) 344:1242552.

BERGER, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–321.

BOLGER, D. T., W. D. NEWMARK, T. A. MORRISON AND D. F. DOAK. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

BUNNEFELD, N. ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

CHAPMAN, B. B., C. BRÖNMARK, J.-Å. NILSSON AND L.-A. HANSSON. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

DECESARE, N. J. ET AL. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

DOAK, D. F., V. J. BAKKER, B. E. GOLDSTEIN AND B. HALE. 2014. What is the future of conservation? Trends in Ecology & Evolution 29:77–81.

FRYXELL, J., J. GREEVER AND A. SINCLAIR. 1988. Why Are Migratory Ungulates so Abundant. American Naturalist 131:781–798.

FRYXELL, J. M. AND A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241.

GILLIS, E. A., D. J. GREEN, H. A. MIDDLETON AND C. A. MORRISSEY. 2008. Life history correlates of alternative migratory strategies in american dippers. Ecology 89:1687–1695.

GORDON, I. J., A. J. HESTER AND M. FESTA-BIANCHET. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

GRAYSON, K. L., L. L. BAILEY AND H. M. WILBUR. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. Ecology 92:1236–1246.

HEBBLEWHITE, M., E. MERRILL AND G. MCDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

JOHNSON, H. E., M. HEBBLEWHITE, T. R. STEPHENSON, D. W. GERMAN, B. M. PIERCE AND V. C. BLEICH. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

JOHNSON, H. E., L. S. MILLS, T. R. STEPHENSON AND J. D. WEHAUSEN. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

JOHNSON, H. E., L. S. MILLS, J. D. WEHAUSEN, T. R. STEPHENSON AND G. LUIKART. 2011. Translating Effects of Inbreeding Depression on Component Vital Rates to Overall Population Growth in Endangered Bighorn Sheep. Conservation Biology 25:1240–1249.

KAITALA, A., V. KAITALA AND P. LUNDBERG. 1993. A Theory of Partial Migration. American Naturalist 142:59–81.

KAREIVA, P. AND M. MARVIER. 2012. What is Conservation Science? BioScience 62:962–969.

LUNDBERG, P. 1987. Partial bird migration and evolutionarily stable strategies. Journal of Theoretical Biology 125:351–360.

LUNDBERG, P. 1988. The evolution of partial migration in Birds. Trends in Ecology & Evolution 3:172–175.

MILNER-GULLAND, E. J., J. M. FRYXELL AND A. R. E. SINCLAIR. 2011. Animal Migration: A Synthesis. OUP Oxford.

MORRISON, T. A. AND D. T. BOLGER. 2012. Wet season range fidelity in a tropical migratory ungulate. Journal of Animal Ecology 81:543–552.

PULLIAM, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROBINSON, R. A. ET AL. 2009. Travelling through a warming world: climate change and migratory species. Endangered species research 7:87–99.

SKOV, C. ET AL. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society of London B: Biological Sciences 278:1414–1418.

U. S. FISH AND WILDLIFE SERVICE. 2007. Recovery plan for the Sierra Nevada bighorn sheep. U. S. Fish and Wildlife Service, Sacramento, California, USA.

WHITE, K. S., N. L. BARTEN, S. CROUSE AND J. CROUSE. 2013. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

WILCOVE, D. S. AND M. WIKELSKI. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.

CHAPTER 2.

“MigrateR”: EXTENDING NON-LINEAR MODELING METHODS FOR QUANTIFYING MIGRATORY MOVEMENT BEHAVIOR[1]

Animal movement plays a central role in ecology, linking the disciplines twin concerns: distribution and abundance (Van Moorter et al. 2016). The advent of modern animal-tracking technology has empowered researchers to investigate this link in unprecedented detail (Kays et al. 2015). Through these developments migration has come to the fore as an area of research interest and conservation concern. Migratory species are often extremely abundant (Fryxell et al. 1988) exerting a strong influence on ecosystem processes and biodiversity (Bauer and Hoye 2014). Unfortunately, migratory species across a wide range of taxa are also facing global declines that remain poorly understood (Berger 2004; Harris et al. 2009; Robinson et al. 2009).

Defining migration has remained challenging (Dingle and Drake 2007). Migratory behavior is found across a wide array of taxa and is broadly understood as a strategy for exploiting spatial resources that vary cyclically with time. Most research has focused on long-distance migration, but many species migrate across short distances. Migration along steep altitudinal gradients, for example, is common in insects (Gutierrez and Wilson 2014), birds (Boyle et al. 2010), bats (McGuire and Boyle 2013) and ungulates (Albon and Langvatn 1992). Vertical migration of aquatic taxa in lakes and the ocean is also common, but occurs on a daily rather than an annual cycle (e.g. zooplankton Lampert 1989; fish,Beamish 1966; sea turtles, James et al. 2006; sharks, Sims et al. 2006;

---

[1] Intended for submission as an Applications article to Methods in Ecology and Evolution with Mark Hebblewhite, Thomas R. Stephenson and Evelyn H. Merrill as coauthors.

and marine mammals Alves et al. 2010). Despite similarities in migratory behavior across taxa, the definition of migration has remained inconsistent making migratory behavior difficult to compare (Dingle 2006). Indeed, this is even sometimes the case within a single species, like elk *Cervus elaphus*, for example, where 4 recent studies of migration have relied on as many definitions of migratory behavior (Hebblewhite and Merrill 2011; Middleton et al. 2013; Cole et al. 2015; Eggeman, Scott et al. 2016). Such definitions are often ad hoc and/or specific to a study system and thus impossible to generalize or extend. The study of migration would benefit from a consistent definition that allows comparison across taxa while still accommodating species-specific differences in behavior.

Non-linear modeling methods have recently risen in popularity as an alternative to ad-hoc classification (Bunnefeld et al. 2011). These methods are based on net squared displacement (NSD), a metric based in movement theory (Turchin 1998) which measures the square of the straight-line distance between an animal's starting point and each subsequent location. The structure of these models gives each parameter a biological meaning (e.g. the distance, duration and timing of migratory movement), allowing easy interpretation and comparison across taxa. Although NSD-based classification is theoretically promising, practical difficulties have married its implementation to ad-hoc adjustment, requiring many authors to reclassify questionable movement behavior based on subjective visual assessments (e.g. Bischof et al. 2012). As Bunnefeld et al. (2011) note in their original paper, even in simplified simulations, this method frequently misclassifies residency (36% of cases). Börger and Fryxell (2012) provide an improved model for residency (which we also adopt, see below), but residents remain sensitive to misclassification. Seasonal home-range expansion, which is common among species living in seasonal environments (e.g. Lesage et al. 2000; Wiktander et al. 2001; Cronin et al. 2012), creates temporal changes in the variation in NSD, which are often misidentified as migratory or dispersal movements. NSD migration models are tailored to long-distance movements, making the misclassification of migrants a concern where migratory distances are similar to the diameters of seasonal ranges. These models can also be sensitive to starting location because the calculation of all NSD values depends on this point (Bunnefeld et al. 2011). These problems often necessitate ad-hoc reclassification by researchers (Mysterud et al. 2011; Bischof et al. 2012; Naidoo et al. 2012; Jones et al. 2014), reducing the putative benefits of the approach's goal of standardizing classification. Finally, these methods are computationally complex, making them difficult to implement in a consistent fashion, especially for large datasets.

Here, we created the “migrateR” package (available on GitHub; Spitz 2015) for the R statistical environment (R Core Team 2014) to 1) improve NSD models to better account for sensitivity to starting location; 2) adapt NSD models to increase success in classifying altitudinal migration— perhaps the most common form of short-distance migration; and 3) facilitate the application and further refinement of NSD modeling approaches to classifying and quantifying migratory behavior. Accordingly, we illustrate the utility of our expanded approach using elk and federally-endangered Sierra Nevada bighorn sheep *Ovis canadensis sierrae* as examples.

Methods

Adaption of NSD Models

Following Bunnefeld *et al.* (2011) as updated by Börger & Fryxell (2012) we used five *a priori* statistical models each representing a different movement behavior (Figure 2-1). To classify the movement behavior of an animal-year of location data, we compared the fit of these *a priori* models using AIC (Burnham & Anderson 2002) to determine which behavior received the greatest support.

Our first improvement to the original Bunnefeld *et al.* (2011) methods were to rearrange their notation to directly estimate the duration of winter range residency. We made a slight algebraic change to the original models for migration and mixed migration used by Bunnefeld et al. (2011). Thus our modified NSD model of migration (solid blue line in Fig. 1 A) was the double sigmoid:

$$NSD = \frac{\delta}{1+e^{\left(\left(\theta_1 - t\right)/\psi_1\right)}} + \frac{\delta}{1+e^{\left(\left(\theta_1+2*\psi_1+2*\psi_2+\rho-t\right)/\psi_2\right)}} \qquad \text{Eqn 1.}$$

where δ represents the NSD separating seasonal ranges ranges, t represents time, θ indicates the midpoint of fall migration, ψ is the time required to complete ½ to ¾ of the migration (representing the duration of migratory movements) and ρ is the length of time spent on the migratory range. Subscripts on ψ differentiate parameter estimates for departure and return movements. Similarly we represent mixed migration (dashed green line in Fig. 1 A) with:

$$NSD = \frac{\delta_1}{1+e^{\left(\left(\theta_1 - t\right)/\psi_1\right)}} + \frac{\delta_2}{1+e^{\left(\left(\theta_1+2*\psi_1+2*\psi_2+\rho-t\right)/\psi_2\right)}} \qquad \text{Eqn 2.}$$

which includes the addition of subscripts allowing the distance traveled between ranges to vary by season (i.e. representing migration in which the individual doesn't fully return to the original range). Instead of estimating the timing (midpoint) of return movement (as in Bunnefeld et al. 2011),our models included the duration of occupancy on migratory range as a directly estimated parameter. We argue that the direct estimate of the duration of winter range occupancy is more useful as it can be used to directly inform our definition of migration, providing a consistent quantitative basis for excluding exploratory out-and-back movements from classification as migratory movement. This additional criterion can be included either as an *a priori* restriction of model fitting based on expected range of winter range residency or as an *a priori* decision rule implemented after model fitting. For example, many researchers have defined a minimum time of residency as a criterion for defining migration, e.g., individuals needed to spend > 30 days on a summer range to be defined as a migrant (Eggeman et al. 2016, see also Cagnacci et al. 2011). The structure of these models was otherwise equivalent to those used by Bunnefeld et al. (2011). The midpoint of return migration (θ_2, omitted from our models) can be calculated as a derived parameter ($\theta_2 = \theta_1 + 2*\psi_1 + 2*\psi_2 + \rho$).

We represented dispersal (dotted purple line in Fig. 1 A) with a single sigmoid (i.e. movement with no return):

$$NSD = \frac{\delta}{1+e^{((\theta-t)/\psi)}} \qquad \text{Eqn 3.}$$

where parameters are interpreted identically as in the migrant model, but ψ represents the midpoint of dispersal movement rather than migration (Bunnefeld et al. 2011). Following improvements made by Börger and Fryxell (2012) we represented residency (dashed red line in Fig. 1A) as:

$$NSD = \delta * \left(1 - e^{(\theta * t)}\right) \qquad \text{Eqn 4.}$$

Where δ represents the mean NSD of resident range locations, t is time and θ is the logarithm of the rate constant (see Börger and Fryxell 2012 for an explanation of this term's interpretation). Finally, we represented nomadic behavior (dashed yellow line in Fig. 1 A) with the linear model:

$$NSD = \beta * t \qquad \text{Eqn 5.}$$

where β is a constant and t is time, and a linearly increasing NSD represents the expectation from a randomly moving individual under diffusion-based movement (Turchin 1998).

<u>Adapted Elevation Models</u>

Classification of migratory behavior using the NSD approach only includes spatial information from the two horizontal dimensions of a Cartesian plane. However, many species migratory movements follow a third vertical dimension, usually altitude (but also depth in aquatic organisms). Compared to NSD we expected altitudinal movements to show weaker temporal patterns of variance, making shorter migration movements easier to detect. Therefore, we modified our NSD movement models to be fit to elevation, developing three models each representing a different movement behavior (Figure 2-1; Chapter 2). We omitted nomad and mixed-migrant models as expectations for these behaviors with respect to elevation are unclear, but Eqn. 2 could be easily adapted if there were biological rationale for mixed elevational migrants, for example. Where possible, we parameterized these models to be directly comparable with our NSD approach, above. The model for migration (solid blue line in Fig 1. B) was represented as the double sigmoid:

$$elevation = \gamma - \frac{\delta}{1+e^{\left(\left(\theta_1 - t\right)/\psi_1\right)}} + \frac{\delta}{1+e^{\left(\left(\theta_1 + 2*\psi_1 + 2*\psi_2 + \rho - t\right)/\psi_2\right)}} \qquad \text{Eqn 6.}$$

where γ represents the average elevation of the starting range, δ represents the difference in elevation between ranges, t represents time, θ indicates the midpoint of fall migration, ψ is the time required to complete ½ to ¾ of the migration (representing the duration of migratory movements) and ρ is the length of time spent on the migratory range. Subscripts on ψ differentiate parameter estimates for departure and return movements and, as above, the midpoint of spring migration (θ_2) can be calculated as $\theta_1 + 2*\psi_1 + 2*\psi_2 + \rho$. Additionally, to allow analysis of incomplete animal-years of data we also included a “one way” model (analogous to the NSD disperser model, Eqn. 3) to quantify unidirectional elevational movements. This one-way model (dotted purple line in Fig. 1 B) was parameterized as the single sigmoid:

$$elevation = \gamma - \frac{\delta}{1+e^{\left(\left(\theta - t\right)/\psi\right)}} \qquad \text{Eqn 7.}$$

and its parameters are interpreted identically as in the migrant model. The model we used for residency (dashed red line in Fig. 1 B) was:

$$elevation = \gamma \qquad \text{Eqn 8.}$$

where γ is a constant. Unfortunately, the difference between NSD and elevation prevents the direct comparison of fit between NSD-based and elevation-based models using AIC

Sensitivity to Start Date

We developed and automated a method for applying model selection criteria to test for and correct sensitivity of NSD models to start date, which we (see example, below; Table 2-1) and others have demonstrated can influence the fit of NSD-based models (see, e.g., Naidoo et al. 2012). An explicit assumption of the NSD method is that the starting point from which NSD is calculated occurs within an individual's seasonal range (Bunnefeld et al. 2011). Many migrants, however, make exploratory movements either outside of their home range or between seasonal home ranges prior to migration (e.g. visiting a winter range during summer or fall). This behavior may be especially common among short-distance migrants (e.g., Chapter 3) and can confuse the classification of animal movement. Our approach is based on the calculation of what we term Relative Net Squared Displacement (rNSD), the net squared displacement relative to a chosen reference point (i.e., other than the starting location; NSD is equivalent to rNSD when the reference date = 1). rNSD can thus be directly compared to NSD as both terms are in the same units (km^2) and are calculated from identical data. We then test for sensitivity to start date by calculating rNSD across a range of dates, fitting NSD models to the rNSD from each of these dates, comparing the minimum AIC across dates and choosing the reference date that results in the lowest AIC score. Relying on the best-supported rNSD should relax the need for assumptions about the first location, thereby improving model fit and ensuring a stable and consistent classification of individual migration behavior. We illustrate the resulting changes in classification and parameter estimates in our example below.

Example: Elk and Bighorn Sheep

We classified movement behavior of n = 80 elk in Alberta, Canada, and 88 federally endangered Sierra Nevada bighorn sheep in three ways, based on: 1) NSD; 2) rNSD; 3) elevation. We then compared animal-year classification across these methods as well as difference in estimates of timing parameters for animal-years classified as migrant by more than one approach. For details on the location data used, see Hebblewhite *et al.* (2006, 2008) and Chapter 3. Following Bunnefeld *et al.* (2011) we subsampled the elk data to one point per day (the full elk data set is available on MOVEBANK project ID 72264071; we include only the subsampled data in this package). We withheld animal-years classified by NSD-based models as dispersers and nomads from this comparison because we do not have ecologically-meaningful elevation-based models of these movement behaviors. For purposes of our comparison we also treated migrant and mixed-migrant classification as equivalent (i.e. both strategies represent a form of migration) to facilitate comparison between elevation and NSD models. Full code for this example is available in Appendix S1.

We fit NSD and elevation models using the `mvmtClass` function in the package migrateR. This function takes an animal movement trajectory as input (with spatial coordinates, timestamp and, optionally, elevation values for each location, see help from the well documented “adehabitatLT” package; Calenge 2006) and outputs an object of class `mvmt` which includes movement models fit to the animal-year's (the sample unit) location data. By default, standard NSD models are fit, but elevation-based models can be fit instead by setting the optional argument `typ` equal to `elev`. To fit both NSD and altitudinal models to our elk data we used the commands:

```
mvmtClass(elk)
mvmtClass(elk, typ=”elev”)
```

By default, `mvmtClass` assumes migration can't occur before the first location observed ($\theta > 0$) and restricts the duration of migratory movements ($1 \leq \psi \leq 21$ days; total duration of migration ~ 4 ψ, i.e., 4 to 84 days). We relied on these defaults in this example, but they can be changed using the `p.est` argument, which handles constraints on parameter estimates as well as starting values.

To find the reference date for the best supported rNSD, we used the function `findrdt`. By default this function calculates rNSD for up to 15 dates, one for each of the first 15 days following the start date during which a location was recorded. It then fits NSD models to NSD and the rNSD calculated for each of these dates and compares them using AIC, returning the record number of the reference location. To fit models to the best-supported rNSD we therefore used:

```
elk.rdt <- findrdt(elk)
elk.rsd <- mvmtClass(elk, refdt=elk.rdt)
```

The resulting movement class objects can be plotted separately using the `plot` function, e.g.:

```
plot(elk.rsd[[1]])
```

or plotted sequentially using:

```
sapply(elk.rsd,plot)
```

Once models are fit, the top model from a `mvmt` object can easily be identified using the `topmvmt` function, which compares AIC values to determine the movement model with the greatest support. We determined the best-supported movement models using, e.g.:

```
topm.elk <- topmvmt(mvmtClass(elk))
```

which provides a list of models. We then extracted the classifications using

```
names(topm.elk)
```

We found differences in NSD and RSD classification in both elk and bighorn sheep (Table 2-1; see Figure 2-2 for example plots). Classification between these two methods disagreed in 8% of elk and 24% of bighorn of animal-years (95% confidence intervals 0.00 – 0.18 and 0.15 – 0.33, respectively), highlighting that in using NSD-based metrics sensitivity to starting location can be species-specific and that this creates greater difficulty in the classification of bighorn than in the classification of elk. We also found differences in classification between NSD and elevation methods in both elk and bighorn sheep (Table 2-2; see Figure 2-3 for example plots). Classification by NSD and elevation differed in 12% of elk animal-years (95% confidence interval: 0.00 – 0.24) and 24% of animal-years for bighorn sheep (95% confidence interval: 0.15 – 0.33).

These results understate the difference in the methods we consider, because these methods can produce consistent classifications while providing very different descriptions of migratory behavior. Where classification agreed, we found no consistent directional differences in the estimates of parameters by NSD and RSD, but on average NSD and RSD models differed by more than two weeks in their estimates of migratory timing and more than 12 days in their estimates of winter range residency for both species (Table 2-3). In contrast, we found consistent directional differences between parameter estimates from NSD and elevation models (Table 2-3). Compared to NSD, elevation models estimated earlier occurrence of migration in both elk and bighorn (by 34.5 and 16.5 days respectively) and estimated longer occupancy in elk (by 36.7 days) but shorter occupancy in bighorn sheep (by 21.8 days; Table 2-3). Finally, compared to NSD, elevation models also estimated that outgoing migratory movement by bighorn sheep lasted longer, taking an additional 4.6 days to complete ½ to ¾ of the movement but that return movements for bighorn were shorter (taking 4.5 fewer days to complete ½ to ¾ of the movement; Table 3). Thus, even where these methods agree in their classification, they differ significantly in their characterization of migratory movement.

Discussion

Our example analyses illustrate migrateR's ability to allay three common problems with previous model-driven methods of classifying migratory movement. First, our results show that our rNSD-based models can circumvent NSD's sensitivity to choice of starting location. Second, we show that our elevation-based models are capable of detecting small-distance movements that are invisible to the NSD approach. Third, our improvements address the noted bias of NSD models against classifying movement as resident. Both rNSD and elevation-based methods classified more individuals as resident than did NSD methods. More importantly though, our re-parameterization of movement models to directly estimate the length of an individual's residency (ρ) on the migratory range, provides a quantitative and biologically meaningful basis for evaluating whether migrant classification is appropriate. Finally, we have greatly increased the ease with which these methods can be implemented, including tools for plotting and other visual checks. By making NSD, rNSD and elevation-based methods more accessible through migrateR we hope to foster the further refinement of methods for the classification and quantification of migratory behavior.

There has been great interest in the potential of non-linear modeling for the classification of animal movement, yet these methods have remained under used. Although nearly 50 publications have cited Bunnefeld et al (2011) in the 4 years since it was published, fewer than a third of these studies employ the papers' analytical approach. Given the complexity of implementing these methods, it should come as no surprise that nearly half of the papers to employ model-driven classification have included as coauthor one or more of the methods original authors. Initial applications strongly favored ungulates, particularly moose *Alces alces*, (Neumann et al. 2012, 2013; van Moorter et al. 2013; White et al. 2013) red deer/elk (Mysterud et al. 2011; Bischof et al. 2012; Allen et al. 2014; Eggeman, Scott et al. 2016) and roe deer *Capreolus capreolus* (Mysterud et al. 2012; Gaudry et al. 2015; Cagnacci et al. 2016), but also caribou *Rangifer tarandus* (DeCesare et al. 2012; Wilson et al. 2014). Recent efforts have broadened the taxonomic application of this approach to include successful quantification of long-distance migration in birds (Beatty et al. 2013, 2015; Kesler et al. 2014; Leopold and Hess 2014) and reptiles (Blake et al. 2013). Despite this broad success, there are also systems in which this approach has so far proved inadequate (elk in western Wyoming; Jones et al. 2014). While there is reason to be optimistic about the further extension of model-driven movement classification, the diversity of animal migratory behavior will require us to further refine and vary these methods. Our open-source migrateR package, housed on the openly accessible and editable gitHub repository, will provide a consistent software platform for researchers of animal migration to continue to refine and adapt classification methods.

The incremental improvements we illustrate highlight current ambiguity in the treatment of migratory data, but also provide promising avenues for further improvement. Appropriately matching mathematical models to ecological phenomenon is always challenging and is critical to rigorous hypothesis testing (Levins 1966). It is incumbent on us as researchers to use our knowledge of biology to choose an analytical approach appropriate to the questions we treat. Our goal with migrateR was to expand existing methods for quantifying migration and other animal movement behavior to better match statistical models to animal-movement data. Our elevation-based approach illustrates how other approaches to quantifying migratory behavior can complement existing NSD-based approaches, characterizing aspects of this behavior that would remain invisible to NSD modeling alone. This approach may be particularly useful to the study of migration in insects, birds and bats previously identified as altitudinal migrants (Inouye et al. 2000; Hahn et al. 2004; Rice 2008; McGuire and Boyle 2013; Gutierrez and Wilson 2014). The models we include here are, of course, not exhaustive. The approach we illustrate with elevation can be extended to an arbitrary Cartesian axis (e.g. Bartlam-Brooks et al. 2013), other univariate ecological gradients (e.g. distance from water; Naidoo et al. 2012) or even more comprehensive non-Cartesian measures (see Peters et al. 2016). More simply, the elevation models we supply could easily be applied to compare the timing of diel-vertical migration among different members of an aquatic food chain (e.g. Beamish 1966; Lampert 1989; James et al. 2006; Sims et al. 2006; Alves et al. 2010). Matching mathematical models to the biology of migratory systems in this way will improve our ability to meaningfully classify and quantify a wider variety of migratory behaviors within a framework that facilitates comparison. Incremental improvements such as those we propose allow for closer correspondence between data and models, reducing the necessity of ad-hoc oversight and thereby increasing the rigor with which migration can be treated.

Even with these improvements, there will still be cases where appropriate classification of an animal's movement remains unclear. In these situations, we can look to the differences among classification for valuable clues to the ecological drivers underlying this behavior (Cagnacci et al. 2016). Although it may be tempting to rely on simulations to adjudicate these conflicts (e.g. Bunnefeld *et al.* 2011), simulating movement data presupposes precisely the underlying mechanisms we are seeking to identify and understand. Although simulations provide the convenience of a known “truth”, we believe it is the messy work of struggling to classify ambiguous animal-movement data that promises the greatest strides forward in how we understand the mechanisms underlying migration. Only when these mechanisms are better understood can classification methods be meaningfully compared through the iterative evaluation of realistic simulations. As Cagnacci et al. (2016) emphasize, the search for truth in the classification of migration may prove far too elusive because of the myriad of mechanisms driving the behavior, and, instead, comparisons of migratory behavior and drivers across populations–facilitated by our approach –may be a productive route.

References

ALBON, S. AND R. LANGVATN. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502–513.

ALLEN, A. M., J. MÅNSSON, A. JARNEMO AND N. BUNNEFELD. 2014. The impacts of landscape structure on the winter movements and habitat selection of female red deer. European Journal of Wildlife Research 60:411–421.

ALVES, F., A. DINIS, I. CASCÃO AND L. FREITAS. 2010. Bryde's whale (Balaenoptera brydei) stable associations and dive profiles: New insights into foraging behavior. Marine Mammal Science 26:202–212.

BARTLAM-BROOKS, H. L. A., P. S. A. BECK, G. BOHRER AND S. HARRIS. 2013. In search of greener pastures: Using satellite images to predict the effects of environmental change on zebra migration. Journal of Geophysical Research: Biogeosciences 118:1427–1437.

BAUER, S. AND B. J. HOYE. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science (New York, N.Y.) 344:1242552.

BEAMISH, F. W. H. 1966. Vertical Migration by Demersal Fish in the Northwest Atlantic. Journal of the Fisheries Research Board of Canada 23:109–139.

BEATTY, W. S. ET AL. 2015. An empirical evaluation of landscape energetic models: Mallard and American black duck space use during the non-breeding period. The Journal of Wildlife Management 79:1141–1151.

BEATTY, W. S., D. C. KESLER, E. B. WEBB, A. H. RAEDEKE, L. W. NAYLOR AND D. D. HUMBURG. 2013. Quantitative and Qualitative Approaches to Identifying Migration Chronology in a Continental Migrant. PLoS ONE 8:e75673.

BERGER, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–321.

BISCHOF, R., L. E. LOE, E. L. MEISINGSET, B. ZIMMERMANN, B. VAN MOORTER AND A. MYSTERUD. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist 180:407–424.

BLAKE, S. ET AL. 2013. Vegetation dynamics drive segregation by body size in Galapagos tortoises migrating across altitudinal gradients. Journal of Animal Ecology 82:310–321.

BÖRGER, L. AND J. M. FRYXELL. 2012. Quantifying individual differences in dispersal using the net squared displacement statistics:222 – 230.

BOYLE, W. A., D. R. NORRIS AND C. G. GUGLIELMO. 2010. Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society of London B: Biological Sciences 277:2511–2519.

BUNNEFELD, N. ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

CAGNACCI, F. ET AL. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

CAGNACCI, F. ET AL. 2016. How many routes lead to migration? Comparison of methods to assess and characterize migratory movements. Journal of Animal Ecology 85:54–68.

CALENGE, C. 2006. The package "adehabitat" for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

COLE, E. K. ET AL. 2015. Changing migratory patterns in the Jackson elk herd. The Journal of Wildlife Management 79:877–886.

CRONIN, M., P. POMEROY AND M. JESSOPP. 2012. Size and seasonal influences on the foraging range of female grey seals in the northeast Atlantic. Marine Biology 160:531–539.

DECESARE, N. J. ET AL. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

DINGLE, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147:212–220.

DINGLE, H. AND V. A. DRAKE. 2007. What Is Migration? BioScience 57:113–121.

EGGEMAN, SCOTT, M. HEBBLEWHITE AND E. H. MERRILL. 2016. Behavioral flexibility in migratory behavior in a long-lived ungulate. Journal of Animal Ecology In Press.

FRYXELL, J., J. GREEVER AND A. SINCLAIR. 1988. Why Are Migratory Ungulates so Abundant. American Naturalist 131:781–798.

GAUDRY, W. ET AL. 2015. Partial Migration or Just Habitat Selection? Seasonal Movements of Roe Deer in an Alpine Population. Journal of Mammalogy 96:502–510.

GUTIERREZ, D. AND R. J. WILSON. 2014. Climate conditions and resource availability drive return elevational migrations in a single-brooded insect. Oecologia

175:861+.

Hahn, T., K. Sockman, C. Breuner and M. Morton. 2004. Facultative Altitudinal Movements by Mountain White-Crowned Sparrows (Zonotrichia leucophrys oriantha) in the Sierra Nevada. The Auk:1269–1281.

Harris, G., S. Thirgood, J. G. C. Hopcraft, J. P. G. M. Cromsigt and J. Berger. 2009. Global decline in aggregated migrations of large terrestrial mammals. Endangered Species Research 7:55–76.

Hebblewhite, M. and E. H. Merrill. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870.

Inouye, D. W., B. Barr, K. B. Armitage and B. D. Inouye. 2000. Climate change is affecting altitudinal migrants and hibernating species. Proceedings of the National Academy of Sciences 97:1630–1633.

James, M. C., C. A. Ottensmeyer, S. A. Eckert and R. A. Myers. 2006. Changes in diel diving patterns accompany shifts between northern foraging and southward migration in leatherback turtles. Canadian Journal of Zoology 84:754–765.

Jones, J. D., M. J. Kauffman, K. L. Monteith, B. M. Scurlock, S. E. Albeke and P. C. Cross. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769–1779.

Kays, R., M. C. Crofoot, W. Jetz and M. Wikelski. 2015. Terrestrial animal tracking as an eye on life and planet. Science 348:aaa2478.

Kesler, D. C. et al. 2014. Effects of satellite transmitters on captive and wild mallards. Wildlife Society Bulletin 38:557–565.

Lampert, W. 1989. The Adaptive Significance of Diel Vertical Migration of Zooplankton. Functional Ecology 3:21–27.

Leopold, C. R. and S. C. Hess. 2014. Corridor- and stopover-use of the Hawaiian goose (Branta sandvicensis), an intratropical altitudinal migrant. Journal of Tropical Ecology 30:67–78.

Lesage, L., M. Crête, J. Huot, A. Dumont and J.-P. Ouellet. 2000. Seasonal home range size and philopatry in two northern white-tailed deer populations. Canadian Journal of Zoology 78:1930–1940.

Levins, R. 1966. Strategy of Model Building in Population Biology. American Scientist 54:421–&.

McGuire, L. P. and W. A. Boyle. 2013. Altitudinal migration in bats: evidence, patterns, and drivers. Biological Reviews 88:767–786.

Middleton, A. D. et al. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

van Moorter, B., N. Bunnefeld, M. Panzacchi, C. M. Rolandsen, E. J. Solberg and B.-E. Sæther. 2013. Understanding scales of movement: animals ride waves and ripples of environmental change. Journal of Animal Ecology 82:770–780.

Mysterud, A., R. Bischof, L. E. Loe, J. Odden and J. D. C. Linnell. 2012. Contrasting migration tendencies of sympatric red deer and roe deer suggest multiple causes of migration in ungulates. Ecosphere 3:art92.

Mysterud, A., L. E. Loe, B. Zimmermann, R. Bischof, V. Veiberg and E. Meisingset. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos 120:1817–1825.

Naidoo, R., P. Du Preez, G. Stuart-Hill, M. Jago and M. Wegmann. 2012. Home on the Range: Factors Explaining Partial Migration of African Buffalo in a Tropical Environment. PLoS ONE 7:e36527.

Neumann, W. et al. 2012. Difference in spatiotemporal patterns of wildlife road-crossings and wildlife-vehicle collisions. Biological Conservation 145:70–78.

Neumann, W., G. Ericsson, H. Dettki and V. C. Radeloff. 2013. Behavioural response to infrastructure of wildlife adapted to natural disturbances. Landscape and Urban Planning 114:9–27.

Peters, W. et al. 2016. Migration across the realized ecological niche in space and time by a large herbivore. Ecological Monographs.

R Core Team. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, C. G. 2008. Seasonal Altitudinal Movements of Mountain Goats. The Journal of Wildlife Management 72:1706–1716.

Robinson, R. A. et al. 2009. Travelling through a warming world: climate change and migratory species. Endangered species research 7:87–99.

Sims, D. W. et al. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. Journal of Animal Ecology 75:176–190.

Spitz, D. 2015. “migrateR”: tools for animal movement classification.

TURCHIN, P. 1998. Quantitative Analysis of Movement: Measuring and Modeling Population Redistribution in Animals and Plants. Sinauer.

VAN MOORTER, B., C. M. ROLANDSEN, M. BASILLE AND J.-M. GAILLARD. 2016. Movement is the glue connecting home ranges and habitat selection. Journal of Animal Ecology 85:21–31.

WHITE, K. S., N. L. BARTEN, S. CROUSE AND J. CROUSE. 2013. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

WIKTANDER, U., O. OLSSON AND S. G. NILSSON. 2001. Seasonal variation in home-range size, and habitat area requirement of the lesser spotted woodpecker (Dendrocopos minor) in southern Sweden. Biological Conservation 100:387–395.

WILSON, R. R., D. D. GUSTINE AND K. JOLY. 2014. Evaluating Potential Effects of an Industrial Road on Winter Habitat of Caribou in North-Central Alaska. Arctic -Montreal- 67:472–482.

TABLE 2-1. Comparison of classification using NSD and RSD approaches. Results shown are for n = 26 elk (*Cervus elaphus;* A) and n = 88 Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* B). We show the classifications we regard as consistent in bold. Classification appears more consistent for elk (A, 24 of 26) than for bighorn sheep (B, 61 of 88).

A

Elk				**RSD**			
		mixed migrant	migrant	disperser	nomad	resident	total
	mixed migrant	**9**	**0**	0	0	0	9
	migrant	**4**	**11**	0	0	1	16
NSD	disperser	0	0	**0**	0	0	0
	nomad	0	1	0	**0**	0	1
	resident	0	0	0	0	**0**	0
	total	13	12	0	0	1	26

B

Bighorn				**RSD**			
		mixed migrant	migrant	disperser	nomad	resident	total
	mixed migrant	**53**	**4**	3	0	2	62
	migrant	**7**	**4**	1	0	1	13
NSD	disperser	2	2	**1**	0	0	5
	nomad	0	0	1	**0**	2	3
	resident	2	0	1	0	**2**	5
	total	64	10	7	0	7	88

TABLE 2-2. Comparison of classification between NSD and elevation models. Results shown are for n = 26 elk (*Cervus elaphus;* A) and n = 88 Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* B). The cells we consider as representing consistent classification among methods are shown in bold. As with the comparison to RSD, elk show fewer differences in classification (A, 4 of 26) than do bighorn (B, 18 of 88).

A

		Elevation		
		migrant	disperser	resident
NSD	mixed migrant	**7**	1	1
	migrant	**15**	1	0
	disperser	0	**0**	0
	nomad	0	1	0
	resident	0	0	**0**
	total	22	3	1

B

		Elevation			
		migrant	disperser	resident	total
NSD	mixed migrant	**55**	4	3	62
	migrant	**12**	1	0	13
	disperser	3	**2**	0	5
	nomad	1	2	0	3
	resident	2	2	**1**	5
	total	73	11	4	88

TABLE 2-3. Differences in estimates of migration characteristics between NSD fit and fit by RSD and elevation models. Here we include only animal-years that were classified by both methods as either “migrant” or “mixed-migrant”. Results are shown for n = 26 elk (*Cervus elaphus;* A) and n = 88 Sierra Neavada bighorn sheep (*Ovis canadensis sierrae;* B). Our analysis failed to find evidence of difference in estimates of the from NSD and RSD models. We did however find differences between NSD and elevation-based estimates for the timing of migration (theta) and the duration of migratory-range occupancy (rho). We also found differences between elevation and NSD model estimates of the duration of migratory movements for bighorn sheep (psi & psi_2) and returning elk(psi_2).

A

		NSD v RSD			NSD v ELV		
Parameter		Estimate	Mean Diff.	SD of Diff.	Estimate	Mean Diff.	SD of Diff.
timing of departing movement	(θ)	-7.07 (p=0.31, df=23)	14.48	30.97	-34.55 (p=0.0011, df=21)	39.04	38.87
length of winter range residency	(ρ)	5.45 (p=0.36, df=23)	12.06	26.64	36.72 (p=0.0044, df=21)	50.51	40.64
duration of departing movement	(ψ)	-0.1 (p=0.92, df=23)	1.51	4.4	0.54 (p=0.8294, df=21)	8.01	8.22
duration of returning movement	(ψ2)	0.71 (p=0.29, df=23)	0.88	3.18	-3.04 (p=0.1718, df=21)	7.37	7.39

B

		NSD v RSD			NSD v ELV		
Parameter		Estimate	Mean Diff.	SD of Diff.	Estimate	Mean Diff.	SD of Diff.
timing of departing movement	(θ)	-2.83 (p=0.27, df=67)	8.91	19.01	-21.17 (p=0.0029, df=66)	39.32	45.05
length of winter range residency	(ρ)	-2.86 (p=0.43, df=67)	15.44	25.24	-20.02 (p=0.0039, df=66)	43.82	38.27
duration of departing movement	(ψ)	1.01 (p=0.26, df=67)	4.15	6.22	4.6 (p=0, df=66)	6.89	6.96
duration of returning movement	(ψ2)	0.21 (p=0.77, df=67)	2.38	5.25	-5.6 (p=0, df=66)	8.39	6.96

FIGURE 2-1**.** Conceptual illustration of Net/Relative Squared Displacement (NSD) and elevation-based models. The *a priori* model set fit to NSD covers a wider range of movement behaviors, than does the elevation model set. Elevation models shown illustrate downward altitudinal movement, but can also accommodate upward migration. See text for explanation of differences between models.

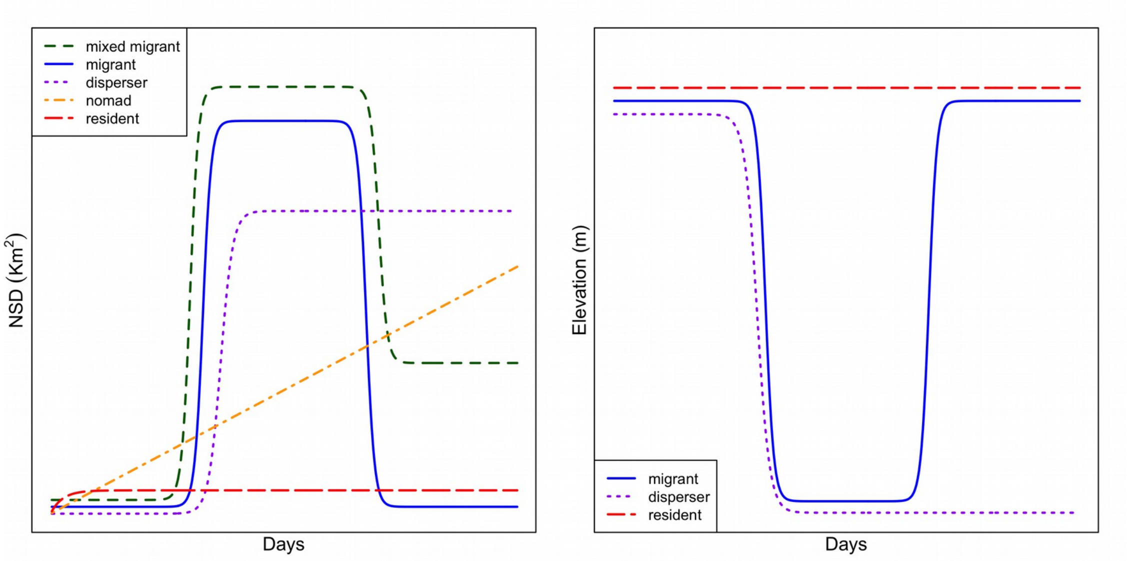
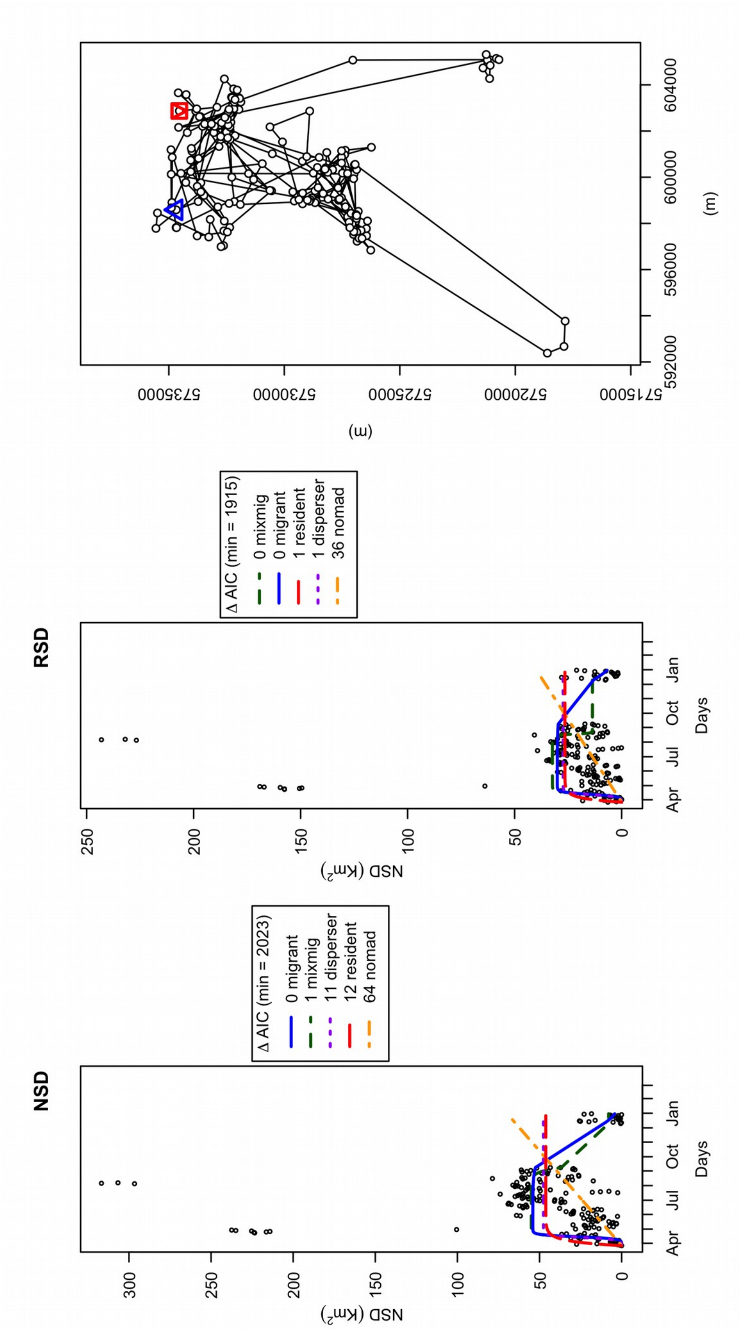


FIGURE 2-2. Illustration of differences in movement classification between NSD and RSD methods. Examples are shown for elk (*Cervus elaphus;* A, left and center panels; reference date = 6), illustrating a change from migrant to resident classification and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* B, left and center panels; reference date =13) showing a change in classification from resident to migrant. While the fit of NSD and RSD models differs little for the elk data, NSD and RSD models for the bighorn show significant differences, with only the RSD model showing the typical “hat-shaped” migrant pattern with empty area under the curve. Note that the range of values shown on the y-axis differs between NSD and RSD plots. In spatial plots (right panels) the first point of the animal movement is denoted by a blue triangle, the last by a red square. RSD classifications receive visual support from the spatial distribution of points. The RSD “resident” elk, shows two exploratory movements (lower right and left), but shows no spatial separation among high-use areas. In contrast,the RSD “migrant” bighorn shows a high-use area (lower right) that is spatially disjunct from other high-use areas.

A


NSD
NSD (Km²)
0
50
100
150
200
250
300
Apr
Jul
Oct
Jan
Days
Δ AIC (min = 2023)
0 migrant
1 mixmig
11 disperser
12 resident
64 nomad
RSD
NSD (Km²)
0
50
100
150
200
250
Δ AIC (min = 1915)
0 mixmig
0 migrant
1 resident
1 disperser
36 nomad
(m)
5715000
5720000
5725000
5730000
5735000
592000
596000
600000
604000
(m)

B

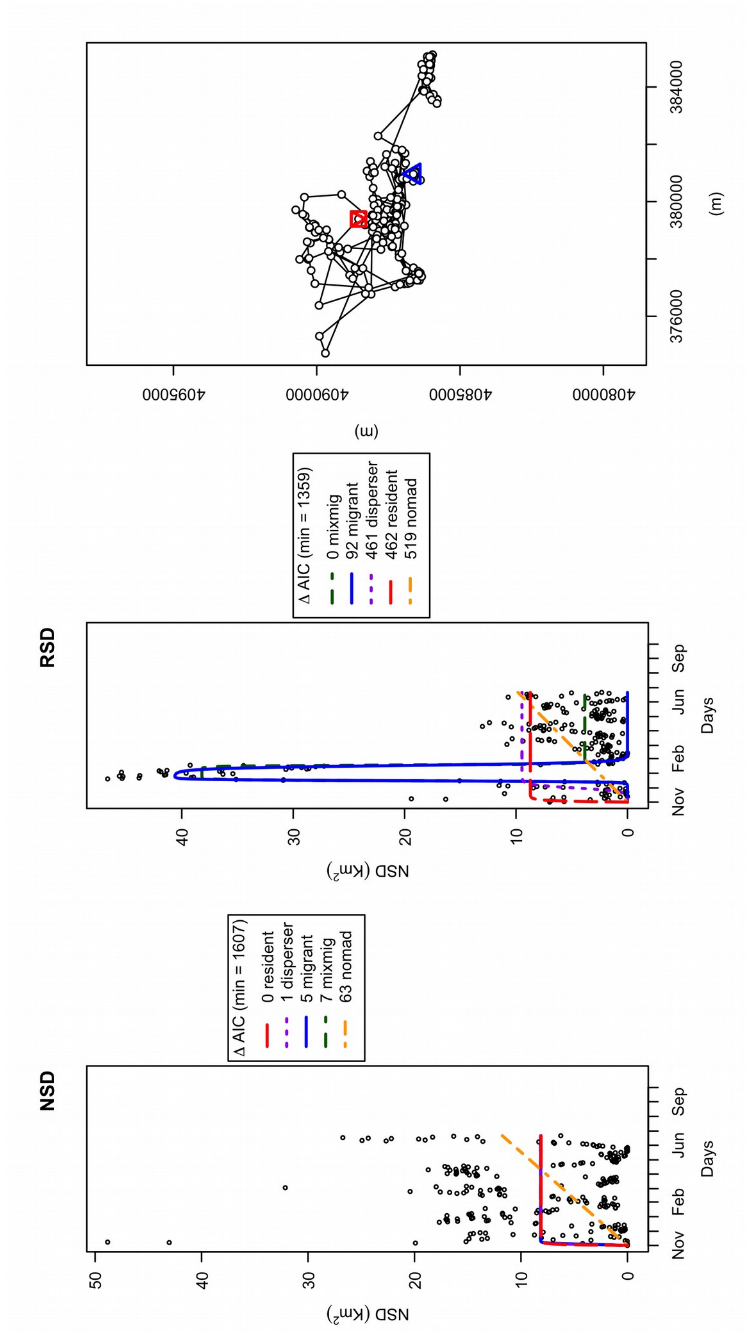
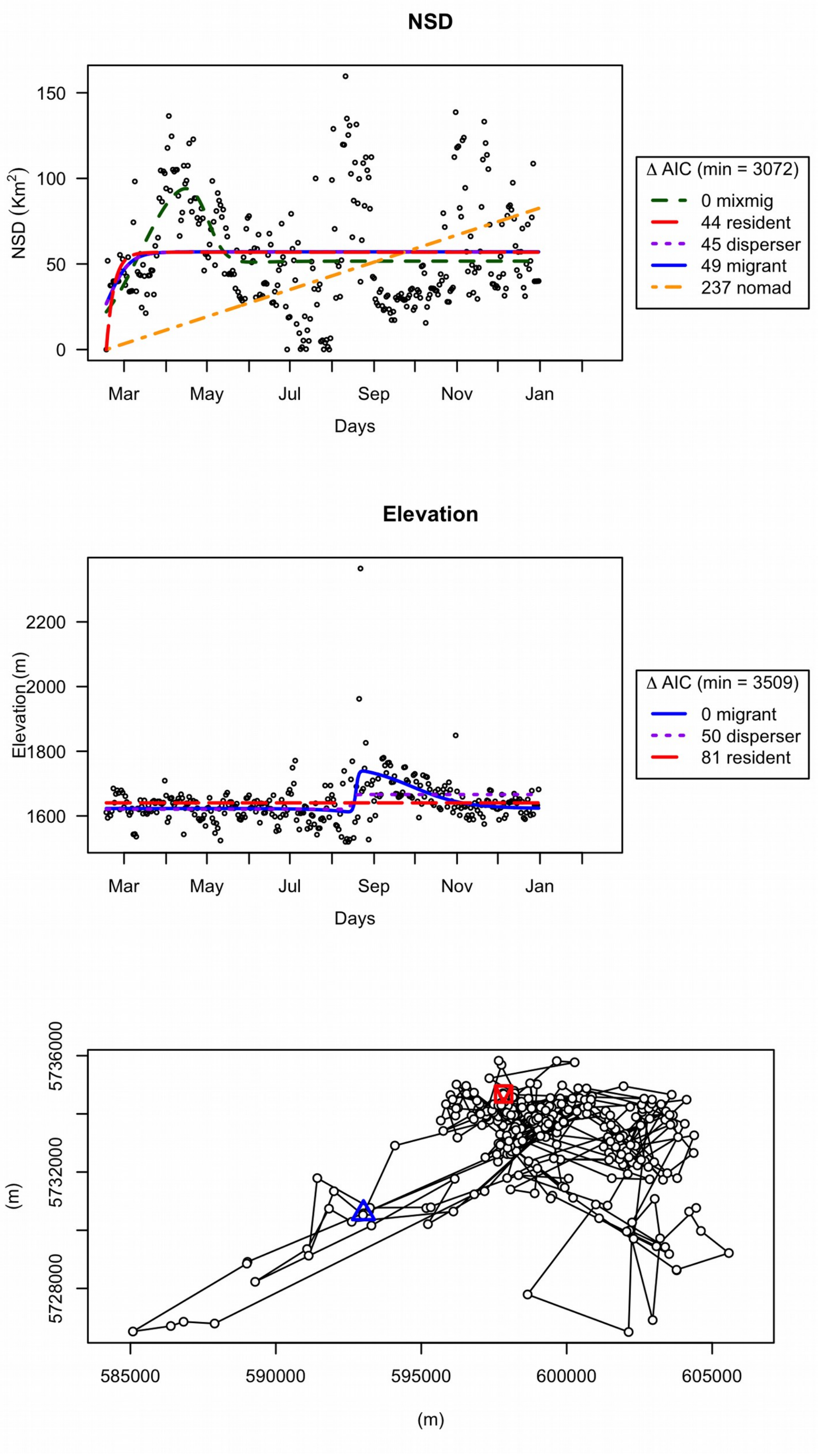
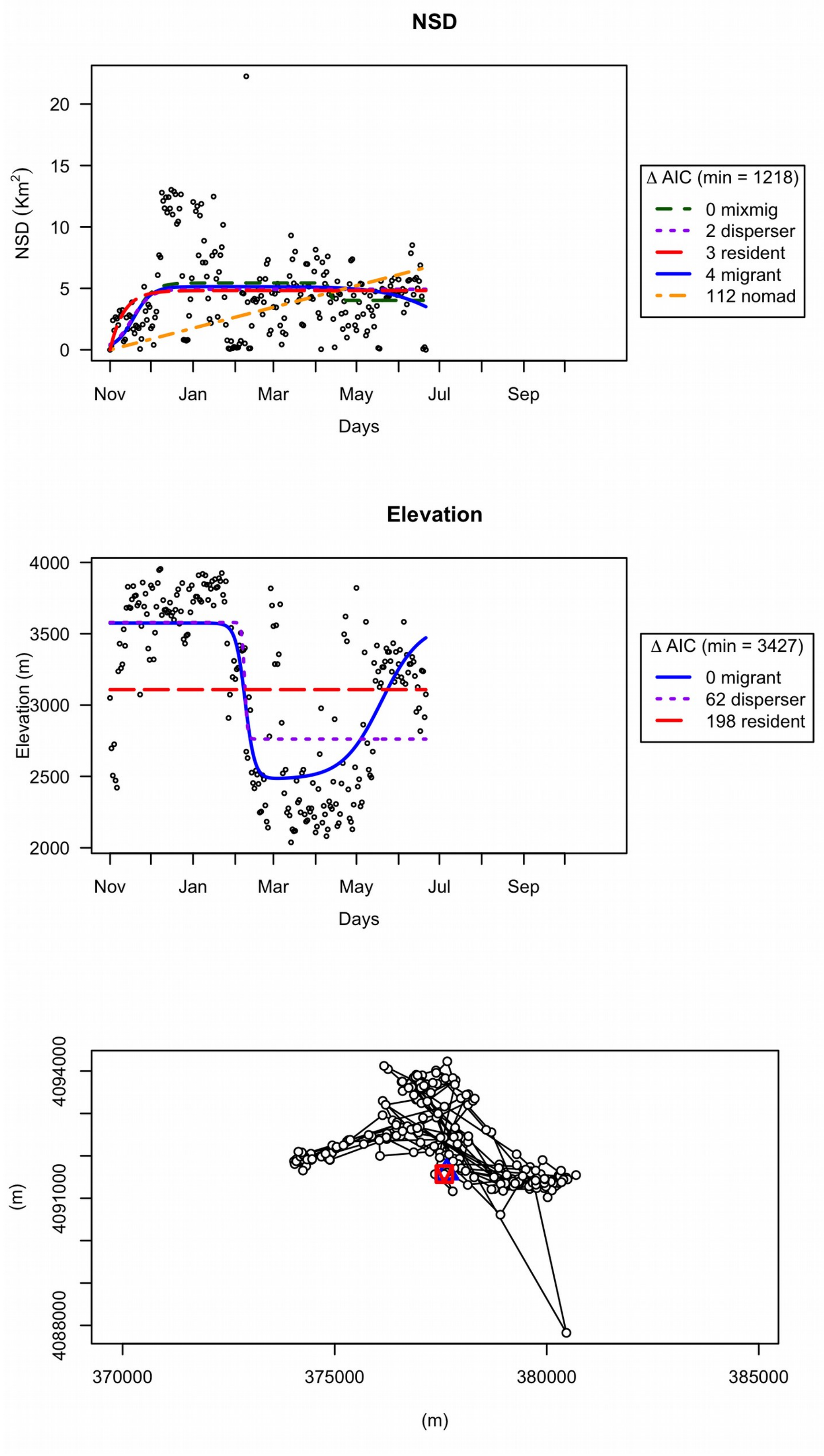

NSD
NSD (Km²)
0
10
20
30
40
50
Nov
Feb
Jun
Sep
Days
Δ AIC (min = 1607)
0 resident
1 disperser
5 migrant
7 mixmig
63 nomad
RSD
NSD (Km²)
0
10
20
30
40
Nov
Feb
Jun
Sep
Days
Δ AIC (min = 1359)
0 mixmig
92 migrant
461 disperser
462 resident
519 nomad
4080000
4085000
4090000
4095000
(m)
376000
380000
384000
(m)

FIGURE 2-3**.** Example of difference in fit and movement classification between NSD and elevation models from elk (*Cervus elaphus;* A) and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* B). Although both methods classify the elk's movement as migrant, their characterization of migratory movement differ starkly. The NSD (mixed) migrant model receives the greatest support showing a departing movement in March, but this model is still a poor fit to NSD, which is highly variable (A, left panel). In contrast elevation values for these movements appear less variable and the elevation-based model for migration fits the data closely, showing a departing movement in August, nearly 5 months after the movement identified by the NSD model (A, center panel). NSD methods classify the bighorn movement as resident (B, left panel), which appears to be supported by the tight spatial grouping of these locations (B, right panel). Elevation models, however, show a clear temporal change in elevation that best supports classification of these movements as migrant.

A


NSD
NSD (Km^2)
150
100
50
0
Mar
May
Jul
Sep
Nov
Jan
Days
Δ AIC (min = 3072)
0 mixmig
44 resident
45 disperser
49 migrant
237 nomad
Elevation
Elevation (m)
2200
2000
1800
1600
Mar
May
Jul
Sep
Nov
Jan
Days
Δ AIC (min = 3509)
0 migrant
50 disperser
81 resident
(m)
5736000
5732000
5728000
585000
590000
595000
600000
605000
(m)

B


NSD
NSD (Km^2)
20
15
10
5
0
Nov
Jan
Mar
May
Jul
Sep
Days
Δ AIC (min = 1218)
0 mixmig
2 disperser
3 resident
4 migrant
112 nomad
Elevation
Elevation (m)
4000
3500
3000
2500
2000
Nov
Jan
Mar
May
Jul
Sep
Days
Δ AIC (min = 3427)
0 migrant
62 disperser
198 resident
(m)
4094000
4091000
4088000
370000
375000
380000
385000
(m)

CHAPTER 3.

HOW PLASTIC IS MIGRATORY BEHAVIOR IN SIERRA NEVADA BIGHORN SHEEP?[2]

As migratory species across a wide array of taxa face global declines, ecologists have shown a renewed interest in developing an understanding of movement behavior that could inform conservation (Berger 2004; Wilcove and Wikelski 2008; Robinson et al. 2009). Migratory behavior allows species to extend their distribution, augmenting their abundance and thereby increasing their ecological influence (Fryxell et al. 1988). Migrants play an important role in ecosystem processes, ferrying resources between ecosystems (Bauer and Hoye 2014). The loss of migratory behavior can thus carry negative consequences for ecosystem processes and species abundance (Gordon et al. 2004). Loss of migration among large herbivores has been especially dramatic (Berger 2004). In Western Canada, for example, Campbell et al (Campbell et al. 1994) report a major shift in plant communities in the twenty years following the extirpation of an endemic migrant (Plains bison, *Bison bison bison*; this period preceded western settlement). More recently, the wildebeest (*Connochaetes taurinus*) of Kruger National park declined by 66% following the instillation of fences blocking migratory routes (Whyte and Joubert 1988). Such reductions in abundance can escalate extinction risk by increasing a species' or population's vulnerability to stochastic events and anthropogenic disturbance (Fagan and Holmes 2006).

---

[2] This chapter is prepared for submission to Journal of Mammalogy with Thomas R. Stephenson and Mark Hebblewhite as coauthors.

Migration is chiefly understood as a behavioral adaptation to temporally variable conditions, with migrants benefiting from access to resources and/or avoidance of predators, parasites, competitors or severe conditions (Bergerud et al. 1984; Fryxell and Sinclair 1988; Boyle et al. 2010; Mysterud et al. 2011). Migratory movements have been characterized by fidelity to multiple seasonal ranges to distinguish this behavior from exploratory or opportunistic forays (Dingle and Drake 2007). Most migratory populations are partially migratory, including an alternative resident strategy where individuals maintain a single seasonal range year-round (Cagnacci et al. 2011; Chapman et al. 2011). There is, however, still disagreement over how partial migration is maintained. If migration and residency are fixed behaviors at the individual level, migrant and resident demography can be treated as separate, a convenient outcome for conservation and management. However, partial migration can also be maintained through a single conditional strategy in which individual behavior is plastic (Lundberg 1988; see, e.g., Adriaensen and Dhondt 1990). Where individual strategy switching is prevalent, a more holistic approach to demography is required, as migrants and residents can no longer be treated conceptually as separate populations. In most taxa, however, the prevalence of strategy switching remains poorly understood.

Plasticity in migratory behavior carries further demographic implications in that this plasticity facilitates behavioral adaptation to changing conditions. Global climate change has fueled speculation that limited plasticity in migratory behavior may make migrants particularly vulnerable to ecological traps (Schlaepfer et al. 2002; Faille et al. 2010; Miller-Rushing et al. 2010). This is particularly a concern among mountain species as alpine ecoregions around the world face accelerated changes in climate and anthropogenic influence (Parmesan 2006; Beever et al. 2011; Chen et al. 2011). These concerns have led to a recent focus on quantifying variation in migratory tactics, i.e., how an individual executes her chosen strategy (e.g. the timing and duration of migratory movements) and the extent to which these tactics are dictated by environmental conditions (Bunnefeld et al. 2011; Monteith et al. 2011; Jones et al. 2014). Research across a number of taxa has also shown plasticity at the level of strategy (i.e. individual adoption of migrant v. resident behavior; e.g. European robin, *Erithacus rubecula*; Adriaensen and Dhondt 1990; or roach *Rutilus rutilus*; Hulthén et al. 2015). In ungulates, results have remained mixed. Numerous studies continue to assume that migratory behavior is fixed at the individual level (e.g. Hebblewhite and Merrill 2011; Middleton et al. 2013), even though this assumption contradicts long-standing knowledge of plasticity in ungulate life history. In a recent critique, Gaillard (2013) brought attention to the paucity of studies that have gathered data over a sufficiently lengthy time frame to test these assertions. Several recent studies appear to support the fixation of migratory strategy, including research by Monteith et al. (2011) on mule deer, *Odocoileus hemionus*, and work by Cole et al. (2015) on elk, *Cervus elaphus.* Over the last few years, however, there have been an increasing number of studies confirming that indeed, individual ungulates can change behavior between years, supporting the need to better understand the scope and causes of migratory plasticity in ungulates (e.g. elk, Eggeman et al. 2016; impala *Aepyceros melampus,* Gaidet and Lecomte 2013; and moose, *Alces* alces, White et al. 2013).

Compared to other ungulates, the migratory behavior of caprids has remained largely under-appreciated and un-quantified. Mountain caprids have long been known to migrate, often along steep altitudinal gradients, but little else is known (Geist 1974). In contrast to cervids, most research on caprid migration has focused on males, but sexual segregation is well documented in this taxon (bighorn sheep, *Ovis canadensis*: Geist 1974; chamois, *Rupicapra rupicapra:* Clarke 1986; mouflon, *Ovis gmelini:* Cransac and Hewison 1997; ibex, *Capra ibex:* Villaret et al. 1997), suggesting that female behavior should be considered separately. Improving our understanding of female migratory behavior may be particularly important to the conservation of migratory ungulates, as females are expected to drive demography in these species (Gaillard et al. 1998). In mountain ungulates in general, migratory behavior is assumed to provide greater access to forage as has been shown in other altitudinal migrants (Albon and Langvatn 1992; Zeng et al. 2010) and may also represent a strategy to minimize predation risk (Festa-Bianchet 1988; Fryxell and Sinclair 1988). Understanding the extent of plasticity in migratory behavior is a necessary step towards evaluating the importance of these proximate drivers.

Linking migratory behavior to species abundance or ecosystem processes requires a clearer understanding of plasticity in migratory behavior. Understanding the extent to which individuals are plastic in their choice of migratory strategy has crucial implications for whether we can treat migrant and resident demography separately or whether we need a more detailed knowledge of migration to inform our analysis of partially migratory populations. Here, we quantify female migratory strategy and tactics across 8 subpopulations of a partially-migratory alpine caprid, the federally-endangered Sierra Nevada Bighorn Sheep (*Ovis canadensis sierrae*, Wehausen and Ramey 2000; Sierra bighorn hereafter). Recent concerns for the recovery of this species have focused on heightened predation risk on the low-elevation winter ranges occupied by migrants (Johnson et al. 2012). In a classic example of apparent competition, non-native deer herds have buoyed populations of cougar (*Puma concolor*), Sierra bighorn's primary predator. Understanding the extent of plasticity in this species will help inform management by clarifying whether these changes to low-elevation winter ranges could threaten the persistence of migratory behavior or Sierra bighorn sub-populations themselves. We then test for 1) evidence of plasticity in individual choice of strategy (i.e. individuals changing between migrant and resident strategies among years); 2) sub-population level differences in strategy prevalence; and 3) sub-population level differences in migratory tactics (timing, duration and separation of migratory movements). Based on life-history theory (e.g., Gaillard 2013) and the few recent studies showing migratory plasticity in ungulates, we hypothesize that Sierra bighorn are plastic in both strategy and tactics and that consequently the prevalence and tactics of migrants vary by subpopulation.

Materials and Methods

Study Area

The Sierra Nevada mountains form the backbone of the state of California, USA, extending 650 km and varying in width from 75 to 125 km (Hill 1975). Current and historical distribution of Sierra bighorn have been limited to the southern half of this range, which contains the bulk of the range's alpine habitat (U. S. Fish and Wildlife Service 2007). The west side of the range rises gradually from 300m (in California's central valley) to over an average of over 3,000 m, including numerous peaks over 4,000 m (Figure 3-1). Unlike their surroundings, peaks of the western Sierra receive significant precipitation and snowfall as moist air masses from the Pacific Ocean are trapped and cooled through orthographic lift. This process creates a rain shadow along the sheer east edge of the range which is consequently more xeric (Hill 1975). The result is steep gradients of temperature, moisture and elevation along the eastern edge of the Sierra Nevada's crest.

We focused on the 8 largest subpopulations of Sierra bighorn, which at the time of data collection represented more than 90% of all bighorn sheep in the subspecies (Figure 3-1). Each subpopulation of Sierra bighorn is believed to share a high-elevation summer range, but whereas some individuals remain year-round high-elevation residents, others migrate to lower-elevation ranges for the duration of winter. By the late 1970s fewer than 150 Sierra bighorn females remained in the wild, surviving in three adjacent subpopulations. The eight subpopulations we analyzed are all descendants of this stock. Although these subpopulations are demographically distinct (Johnson et al. 2010), we do not expect them to be reproductively isolated, because the distances separating subpopulations are smaller than those routinely traveled by rams during the rut (California Department of Fish and Wildlife, unpublished data). Sierra bighorn were placed on the federal endangered species list in 1999 and California Department of Fish and Wildlife has been the lead agency managing the species for recovery (U. S. Fish and Wildlife Service 2007).

Location Data

We captured adult female Sierra bighorn by helicopter net-gun and outfitted them with global positioning system (GPS) collars (University of Montana IACUC AUP 046-11, Federal Fish and Wildlife Service Permit No. TE050122-4). CDFW conducted fall captures from 2005-2010 and 2012-2013, concluding each year by 31 October. For analysis of migratory strategies, we divided GPS data for each animal into one or more biological years, which we defined as beginning 1 November. We subsampled each animal-year to one location per day, choosing the point closest to 16:00h.

To minimize misclassification, we confined our analysis to animal-years with complete winter data, which we defined a priori as beginning before 15 November (i.e. no more than two weeks after the beginning of a migratory year) and ending after April 1 of the following calendar year. We chose the 15 November cut-off to represent Sierra bighorn summer range and to precede the rut, and chose the April 1 end date to include the bulk of the year we believed migrants and residents to occupy separate ranges.

Modeling Altitudinal Movement

Non-linear movement modeling (Bunnefeld et al. 2011) has recently risen in popularity as a method of quantifying and classifying movement behavior (Mysterud et al. 2011; Singh and Ericsson 2014; Eggeman et al. 2016). This approach uses a set of *a priori* models, each representing a different movement behavior, which are then fit to animal location data. Movement behavior can then be classified by comparing the fit of *a priori* movement models to determine which movement behavior received the greatest support. This approach has the advantages of generating parameter estimates that have a direct biological interpretation, are quantitatively standardized, and are comparable across taxa (Bunnefeld et al. 2011). However, these methods are tailored to long-distance movements and have difficulty detecting short-distance migration, for example, across an altitudinal gradient. We adapted *a priori* models of animal movement behavior to be fit to vertical distance using the R package migrateR (elevation; see Chapter 2 for full details). We classified each animal-year by movement strategy in two steps. First we determined the best-supported model for each animal-year using AIC comparison of elevation-based movement models. Second, we used the parameter estimates from these movement models to further restrict classification to a biologically consistent definition of migration. Parameter-based reclassification allows us to compensate for some of the limitations of the modeling methods we employ, while remaining transparent about our assumptions, thus also allowing others to directly replicate our analysis. We then compared the ratio of residents to migrants by sub-population, estimated the overall rate of strategy switching in this population, and quantified the timing, altitudinal distance and duration of migration among Sierra bighorn. We compared the fit of each animal-year of data to elevation-based models. We developed three such non-linear models, each representing a different movement behavior, residency, migration and one-way movement (see Chapter 2). Where possible, these models were parameterized to be directly comparable with previous approaches to quantifying movement behavior. The model for residency was parameterized as:

$$elevation=\gamma \qquad \text{Eqn 1.}$$

where γ is a constant. The model for migration was represented as the double sigmoid:

$$elevation=\gamma-\frac{\delta}{1+e^{((\theta_1-t)/\psi_1)}}+\frac{\delta}{1+e^{((\theta_1+2*\psi_1+2*\psi_2+\rho-t)/\psi_2)}} \qquad \text{Eqn 2.}$$

where γ represents the average elevation of the starting range, δ represents the difference in elevation between ranges, t represents time, θ indicates the midpoint of fall migration, ψ is the time required to complete ½ to ¾ of the migration (representing the duration of migratory movements) and ρ is the length of time spent on winter range. Subscripts on ψ differentiate parameter estimates for fall and spring and the midpoint of spring migration (θ_{Spring}) could be calculated as $\theta+ \psi+ \psi+ \rho$. Additionally, to allow analysis of incomplete animal-years of data we also included a “one way” model to quantify unidirectional elevational movements. This one-way model was parameterized as the single sigmoid:

$$elevation=\gamma-\frac{\delta}{1+e^{((\theta-t)/\psi)}} \qquad \text{Eqn 3.}$$

and its parameters are interpreted identically as in the migrant model. For each animal-year we fit this *a priori* set of non-linear models to elevation as a function of time. In fitting these models, we restricted the range of migratory start dates (θ, minimum = 1) and the duration of migratory movements (ψ, 1 to 21 days; total duration of migration ~ 4 ψ, i.e., 4 to 84 days). We then used AIC to select a top model for each animal-year, assigning an initial movement-behavior classification based on the best-supported model.

We imposed additional constraints on our initial classifications to restrict migration to a consistent biological meaning. To ensure our definition of migration included fidelity to multiple seasonal ranges, we defined minimum thresholds of altitudinal separation ($\delta > 500$m) and occupancy of a second range (>21 days). We reclassified any migrant who did not meet both of these thresholds as resident. We interpreted estimated range occupancy of less than 21 days as representing opportunistic or exploratory forays (i.e. lacking station keeping behavior typical of home range maintenance) rather than migration. These thresholds were chosen post-hoc based on local minima in the distributions of δ and ρ, respectively. For animal-years including forays, we retained the γ estimate from the migratory model, because it better represented mean elevation of the resident winter range.

We further assumed that no Sierra bighorn spend summer on low-elevation ranges. This assumption is consistent with our observations as well as literature on other caprids (Stone sheep, *Ovis dalli stonei*: Seip and Bunnell 1985; mouflon: Dubois et al. 1992; alpine ibex, *Capra ibex ibex*: Grignolio et al. 2004, but chamois, *Rupicapra rupicapra*: Lovari et al. 2006). This assumption had three primary consequences. First, we reclassified low-elevation resident animal-years as migrant. We defined “low-elevation” residents as having a mean elevation (resident γ) below the upper 95% CI of winter elevation for migrants (calculated as $\gamma + \delta$, 2977m). The second consequence of assuming no animals summered at low elevation was that “one-way” animal-years were misclassified. If no animals summer at low-elevation, “one-way” elevational movements are impossible because they must either begin or end on low-elevation summer range.

Consequently, we interpreted “one-way” animal-years as migratory movements where our data were incomplete (i.e. fall or spring movement absent) either due to GPS collar failure, death or misalignment of migratory movement to our definition of migratory year (i.e. fall migration occurs prior to our defined start date of November 1). Accordingly, we reclassified “one way” animal-years as migrant. treating downward movements ($\delta < 0$) as departing (fall) migration and upward movement ($\delta > 0$) as returning movements (spring). The third and final consequence of no individuals summering at low elevation was that any upward migration ($\delta > 0$) we observed must represent cases in which the order of fall and spring migration were reversed. Under our assumption, upward elevational movements in fall would not be possible as they would require that the preceding summer was spent at low-elevation. Upward migration could, however, be observed starting in spring whenever fall migration occurs before the start of an animal-year; in this case the first migratory movement captured would be the (upward) return movement to high elevation in spring, which would then be followed by the (downward) departure from high elevation fall. Consequently, we retained the classification of upward migration as “migrant”, but, changed our interpretation of the timing parameters treating the first movement as the returning (spring) rather than the departing (fall) movement.

Statistical Analyses

We used mixed-effect logistic regression (Hosmer et al. 2013) to estimate the prevalence of strategy switching and to test for sub-population differences in the prevalence of migration. First, we used a model with no fixed effects to quantify the across-subpopulation rate of strategy switching. To test for directional switching, we ran a second model that also included a single fixed-effect term for an individual's starting strategy (the individual's last recorded strategy proceeding each opportunity to switch). This parameter thus allowed us to test whether animals were more likely to switch strategies in a particular direction (either migrant-to-resident or vice versa). We evaluated the statistical significance of these terms based on their associated p-values and evaluated the biological importance of statistically significant terms based on the magnitude of their coefficients. Throughout we included individual as a random effect (to account for individual variation in repeated measures) and excluded data from sub-populations where we only observed one strategy (because both outcomes are required for successful parameter estimation with logistic regression; Hosmer et al. 2013). Second, to test for differences in strategy prevalence by subpopulation, we used a X^2 test for equality of proportions.

Third, to test sub-population level differences in migratory tactics we used mixed-effect linear regression. We analyzed parameter estimates for the timing of migration (θ), the duration of migratory movements (ψ), and vertical distance moved (δ). For each parameter we started with a full model containing terms for each year and population, and then sequentially removed terms through backwards stepwise regression (Hocking 1976). Models for migratory timing (θ) and movement duration (ψ) included both spring and fall terms, with an added fixed effect for season. We tested for differences in the explanatory power of subpopulation and year by using t-tests to compare the mean of the absolute value of Wald statistics for retained year and sub-population terms. We used the

Mt. Baxter sub-population (north to south the centermost migratory sub-population) and 2012 migratory year (the year for which we had the most data) as reference categories. As above, individual was held throughout as a random effect to account for individual variation. All analyses were performed in program R using the adehabitatLT, nlme and migrateR packages (Calenge 2006; R Core Team 2014; Pinheiro et al. 2015; Spitz 2015).

Results

Our classification identified 71 migrant and 30 resident animal-years between 2005 and 2013 (70% and 30% of total animal years, respectively, representing 70 unique individuals, mean number of location-days per animal-year = 290; Figure 3-3). We estimated movement parameters for 61 round-trip migratory movements. The timing of spring migration was nearly twice as synchronous and more than two and a half times as long as fall movements (Table 3-2). The mean date of fall migration was 28 December (95% CI: 10 October to 16 March) and the mean date of spring migration was 9 May (95% CI: 24 March to 25 June). Vertical distances migrated varied from 563 to 1859 (mean =1211) meters and the duration of migratory-range occupancy varied from 23 to 215 days (mean = 101 days; Table 3-2). Mean estimates of year-round resident elevation and summer migrant elevation differed by less than 20m. Seventeen percent of resident animal-years (n=5) included spring forays.

We estimated the rate of individual strategy switching at 0.33 individuals/animal-year (95% CI: 0.16-0.56; Table 3-1). Despite the greater prevalence of the migratory strategy, we observed a nearly equal number of transitions in each direction (migrant-to-resident and vice versa) and were unable to detect directional switching (i.e., a greater tendency to switch strategies in one direction; $p = 0.13$). We did find differences in the prevalence of migratory strategy among sub-populations ($X^2_7 = 39.25$, $p < 1*10^{-5}$). Both resident and migratory strategies were found in 5 of the 8 subpopulations examined, with one subpopulation represented by exclusively resident and two exclusively by migrant animal-years (Gibbs, Wheeler and Bubbs respectively; Figure 3-3).

Our results also provided indirect evidence for plasticity in migratory tactics. The timing, duration and vertical change associated with migratory movements all changed both as a function of sub-population and year. Our top model for migratory timing (θ) included terms for all years but one (2005; Table 3-3). In comparing the relative importance of sub-population and year differences, we found weak evidence that sub-population has a greater influence on timing than did year ($t_{7.4} = 2.04$, $p = 0.079$). Our model of migratory duration (ψ) retained more terms for sub-population (dropping zero) than for year (dropping four; Table 3-3). We were, however, unable to detect a difference in the explanatory importance of the remaining year and sub-population terms ($t_{5.2} = 1.12$, $p = 0.31$). We interpreted these results as indicating that in most years, sub-population plays a greater explanatory role than does inter-annual variation. Our model for the vertical change associated with migration (δ) retained the complete suite of terms (Table 3-3). Thus both sub-population and year explained a significant amount of variation in the vertical separation of seasonal ranges and we were again unable to determine if one of these categories was more important than the other ($t_{10.7} = 0.79$, $p = 0.45$).

Discussion

We find Sierra bighorn to be extremely plastic in migratory strategy and variable in tactics. Migratory propensity and all three tactics we examined—the timing, duration and altitudinal distance of migration—varied both by sub-population and year. Our observations encompassed the extremes of migratory prevalence, including populations in which we observed only migration, migration as a majority behavior, migration as the minority behavior and no migration at all. Population-level differences in migratory prevalence and tactics have been described in a number of other species including moose (Singh et al. 2012), white-tailed deer (Fieberg et al. 2008) and roe deer (Cagnacci et al. 2011). Unlike these study systems, our populations showed no obvious relationship between migratory prevalence and latitude (Figure 3-3). Our description of migratory tactics in bighorn is otherwise largely consistent with descriptions of migratory behavior from other ungulates. Common to mule deer and roe deer, we found that spring migration was more synchronous than fall movements, with fall migration also spanning a greater range of dates (Cagnacci et al. 2011; Monteith et al. 2011).

To our knowledge the annual switching rate we observed is the highest so far recorded for any ungulate and the first such estimate for a caprid. In comparison, switching rates have been estimated at 0.15/animal-year in elk, another mountain ungulate (Eggeman et al. 2016), 0.12 in impala (Gaidet and Lecomte 2013), 0.1 in white-tailed deer (Nelson 1995) and at up to 0.18 in wildebeest, a long-distance tropical migrant whose movements are not altitudinal (Morrison and Bolger 2012). Migrant-resident strategy switching can be conceptualized as a special case of home-range selection (second-order; Johnson 1980) where an individual chooses annually between two overlapping alternatives: the smaller resident or the larger migrant home range (Gaudry et al. 2015). In contrast to the high rate of switching we observed, Dalerum et al. (2007) found a long-distant migrant, caribou, to have high fidelity to the same seasonal range year after year even in the face of extreme habitat alteration. These authors suggest that large home-range sizes allowed caribou to avoid negative demographic consequences of habitat alteration by concentrating within-home-range patterns of habitat selection in areas of consistently high quality. Thus an individual's ability to compensate for changes in within-home-range conditions likely depends both on home range size and environmental stochasticity, with changes in migratory strategy occurring when compensation within the resident range is no longer possible or the additional resources included in the migrant range are non-essential. We should therefore expect rates of strategy switching among species and populations to vary along a continuum. At one extreme, strategy-switching should be rarest where resident ranges are large and/or conditions are constant year-to-year. At the other end of the continuum, strategy-switching should be commonplace where resident ranges are small and/or subject to high inter-annual variation, both of which are true of many populations of Sierra bighorn.

Shorter migration distances may also contribute to plasticity in migratory strategy. As the cost of moving between seasonal ranges approaches zero, we would expect the relative costs and benefits associated with migration in these systems to be determined exclusively by the differences in conditions experienced by the migratory and resident strategies (e.g., differences in climate, forage and predation on high- and low-elevation winter ranges; Fryxell and Sinclair 1988; Mysterud et al. 2011). This is not typically the case for long-distance migrants, where movement itself entails substantial cost. In elk, for example, Hebblewhite and Merrill (Hebblewhite and Merrill 2007) showed that the risk of predation during migration far exceeded the risk experienced by elk on migrant or resident ranges, making the migratory movement the most vulnerable state for elk. Concerted long-distance movement also exacts increased energetic and opportunity costs (i.e. increased caloric demands of locomotion, reduced foraging opportunity during travel; Milner-Gulland et al. 2011). Finally, the cost of travel between ranges often prohibits long-distance migrants from evaluating the quality of both ranges before committing to a strategy (Dingle 2006). In contrast, short-distance migrants like Sierra bighorn may directly assess conditions on both migrant and resident ranges before selecting their strategy. Where travel and information are inexpensive, we should expect greater flexibility in choice of strategy as individuals pursue ideal-free distribution (Fretwell and Lucas 1969).

Our results also underline differences in partial migration among ungulates, suggesting a taxonomic division. For cervids moving along an altitudinal gradient, partial migration typically consists of a shared low elevation winter range, with some individuals migrating to high elevation for summer while others remain resident at low elevation (“low-elevation resident”; red deer, *Cervus elaphus*: Albon and Langvatn 1992; roe deer *Capreolus capreolus:* Mysterud 1999; elk, *Cervus elaphus*: Hebblewhite and Merrill 2007; mule deer, *Odocoilius hemionus*: Monteith et al. 2011; sika deer provide a notable exception: Igota et al. 2004). We observed the opposite of this pattern in Sierra bighorn where summer is the shared range, only migrants retreat to lower elevations for winter and residents remain at high elevations year-round ("high-elevation resident"). Although information on partial migration in caprids is still relatively limited, the pattern of high-elevation residency we observed in Sierra bighorn appears consistent with other observations of ovids (Stone sheep, *Ovis dalli stonei*: Seip and Bunnell 1985; mouflon: Dubois et al. 1992) and of caprids more generally (alpine ibex, *Capra ibex ibex*: Grignolio et al. 2004, but chamois, *Rupicapra* rupicapra: Lovari et al. 2006). The similarities between partial migration in Sierra bighorn and other captrids might lead us to expect higher rates of strategy switching among these species as contrasted, e.g., to cervids.

We may further expect the drivers of high-elevation and low-elevation residency to differ. Traditionally residents have been hypothesized to experience higher predation rates than migrants (e.g. Fryxell and Sinclair 1988; Hebblewhite and Merrill 2007), but this pattern is reversed in systems with high-elevation residents. Upward altitudinal movement is broadly acknowledged as an ungulate predator-avoidance strategy (caribou: Bergerud et al. 1984; elk: Hebblewhite and Merrill 2007; mule deer: Monteith et al. 2011). Nowhere is this consensus clearer than in the literature surrounding caprids, where elevation is assumed to have a central role in predator avoidance ((Geist 1974; Festa-Bianchet 1988; Berger 1991). Consistent with these expectations, Sierra bighorn face the highest predation risk on low-elevation winter range, where they overlap spatially with more abundant herbivore populations capable of supporting predators at higher density (Johnson et al. 2012).

Spatial differences in these costs (e.g. predation) and benefits (e.g. forage) likely underlie the differences we observed in migratory prevalence among subpopulations. We should expect the relative number of residents and migrants in any population to be limited by the amount of habitat suitable for each strategy. The habitat requirements of migrants and residents, however, remain little explored (Bolger et al. 2008). In winter, resident Sierra bighorn are thought to be limited to wind scoured slopes while migrants are expected to depend on rugged terrain below snow line (U. S. Fish and Wildlife Service 2007). This may explain the relative absence of migration at higher latitudes where access to snow-free areas at lower elevation is poor or non-existent. Similarly, the local absence of high-elevation snow-free patches may explain the infrequence of residency at the center of the species' current range. The relative prevalence of single-strategy sub-populations emphasizes the difficulty of studying strategy switching in ungulates.

The high synchrony and prolonged duration we observed in spring migration is consistent with the expectations of the forage maturation hypothesis, where migrants may attempt to maximize forage quality by riding the “green wave” of phenology as it advances upslope in spring (Bischof et al. 2012). The importance of phenology in driving these movements is also suggested by the presence of a similar movement pattern among residents. The resident forays we documented are similar to those observed in other altitudinal migrants, most notably stone sheep (Seip and Bunnell 1985) and red deer (Cagnacci et al. 2011; Mysterud et al. 2011). These excursions suggest that some residents may be able to reap some of the benefits of migration (e.g. access to higher quality forage) while minimizing or avoiding migration's costs (e.g., increased predation risk). The proximity of animal collaring to fall migration may bias high our estimate of migratory timing and overestimate its synchrony. However, this bias should be small and neither effect estimation of spring movements nor strategy classification. We therefore expect it to have no influence on our estimate of the proportion of migrants or rates of strategy switching. A low bias in our estimation of the variance surrounding fall migration would suggest that the contrast in fall and spring synchrony may be even starker than we describe.

The conditional nature of migration among Sierra bighorn challenges the assumptions conventionally applied to the analysis of partially-migratory populations, especially among large herbivores. The high rate of switching we observed suggests that it is inappropriate to assume migrants and residents can be treated conceptually as separate populations with separate vital rates. Unless the demographic consequences of migration and residency are identical, understanding the demography of partially migratory populations like Sierra bighorn requires identifying not only the demographic consequences specific to each strategy, but also the rates at which individuals change strategy and the ecological drivers of these decisions. The data required to address questions of this complexity remains a major challenge in the study of migration. Improving our understanding of migration depends on the increased collection of long-term individual-based data (Bolger et al. 2008; Gaillard 2013).

Literature Cited

ADRIAENSEN, F. AND A. A. DHONDT. 1990. Population-Dynamics and Partial Migration of the European Robin (Erithacus rubecula) in Different Habitats. Journal of Animal Ecology 59:1077–1090.

ALBON, S. AND R. LANGVATN. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502–513.

BAUER, S. AND B. J. HOYE. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science (New York, N.Y.) 344:1242552.

BEEVER, E. A., C. RAY, J. L. WILKENING, P. F. BRUSSARD AND P. W. MOTE. 2011. Contemporary climate change alters the pace and drivers of extinction. Global Change Biology 17:2054–2070.

BERGER, J. 1991. Pregnancy incentives, predation constraints and habitat shifts: experimental and field evidence for wild bighorn sheep. Animal Behaviour 41:61–77.

BERGER, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–321.

BERGERUD, A. T., H. E. BUTLER AND D. R. MILLER. 1984. Antipredator tactics of calving caribou: dispersion in mountains. Canadian Journal of Zoology 62:1566–1575.

BISCHOF, R., L. E. LOE, E. L. MEISINGSET, B. ZIMMERMANN, B. VAN MOORTER AND A. MYSTERUD. 2012. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? American Naturalist 180:407–424.

BOLGER, D. T., W. D. NEWMARK, T. A. MORRISON AND D. F. DOAK. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

BOYLE, W. A., D. R. NORRIS AND C. G. GUGLIELMO. 2010. Storms drive altitudinal migration in a tropical bird. Proceedings of the Royal Society of London B: Biological Sciences 277:2511–2519.

BUNNEFELD, N. ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

CAGNACCI, F. ET AL. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

CALENGE, C. 2006. The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling 197:516–519.

CAMPBELL, C., I. CAMPBELL, C. BLYTH AND J. MCANDREWS. 1994. Bison Extirpation May Have Caused Aspen Expansion in Western Canada. Ecography 17:360–362.

CHAPMAN, B. B., C. BRÖNMARK, J.-Å. NILSSON AND L.-A. HANSSON. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

CHEN, I.-C., J. K. HILL, R. OHLEMÜLLER, D. B. ROY AND C. D. THOMAS. 2011. Rapid Range Shifts of Species Associated with High Levels of Climate Warming. Science 333:1024–1026.

CLARKE, C. 1986. Chamois Movements and Habitat Use in the Avoca River Area, Canterbury, New-Zealand. New Zealand Journal of Zoology 13:175–&.

COLE, E. K. ET AL. 2015. Changing migratory patterns in the Jackson elk herd. The Journal of Wildlife Management 79:877–886.

CRANSAC, N. AND A. J. M. HEWISON. 1997. Seasonal use and selection of habitat by mouflon (Ovis gmelini):Comparison of the sexes. Behavioural Processes 41:57–67.

DALERUM, F., S. BOUTIN AND J. S. DUNFORD. 2007. Wildfire effects on home range size and fidelity of boreal caribou in Alberta, Canada. Canadian Journal of Zoology 85:26–32.

DINGLE, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147:212–220.

DINGLE, H. AND V. A. DRAKE. 2007. What Is Migration? BioScience 57:113–121.

DUBOIS, M., J.-F. GERARD AND M.-L. MAUBLANC. 1992. Seasonal movements of female Corsican mouflon (Ovis ammon) in a Mediterranean mountain range, southern France. Behavioural Processes 26:155–165.

EGGEMAN, S., M. HEBBLEWHITE AND E. H. MERRILL. 2016. Behavioral flexibility in migratory behavior in a long-lived ungulate. Journal of Animal Ecology In Press.

FAGAN, W. F. AND E. E. HOLMES. 2006. Quantifying the extinction vortex. Ecology Letters 9:51–60.

FAILLE, G. ET AL. 2010. Range fidelity: The missing link between caribou decline and habitat alteration? Biological Conservation 143:2840–2850.

FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586.

FIEBERG, J., D. W. KUEHN AND G. D. DELGIUDICE. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. Journal of Mammalogy 89:1529–1539.

FRETWELL, S. D. AND H. L. LUCAS JR. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheoretica 19:16–36.

FRYXELL, J., J. GREEVER AND A. SINCLAIR. 1988. Why Are Migratory Ungulates so Abundant. American Naturalist 131:781–798.

FRYXELL, J. M. AND A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241.

GAIDET, N. AND P. LECOMTE. 2013. Benefits of migration in a partially-migratory tropical ungulate. BMC Ecology 13:36.

GAILLARD, J.-M. 2013. Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. Ecology 94:1261–1264.

GAILLARD, J.-M., M. FESTA-BIANCHET AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

GAUDRY, W. ET AL. 2015. Partial Migration or Just Habitat Selection? Seasonal Movements of Roe Deer in an Alpine Population. Journal of Mammalogy 96:502–510.

GEIST, V. 1974. Mountain Sheep: A Study in Behavior and Evolution. University of Chicago Press.

GORDON, I. J., A. J. HESTER AND M. FESTA-BIANCHET. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

GRIGNOLIO, S., I. ROSSI, B. BASSANO, F. PARRINI AND M. APOLLONIO. 2004. Seasonal variations of spatial behaviour in female Alpine ibex (Capra ibex ibex) in relation to climatic conditions and age. Ethology Ecology & Evolution 16:255–264.

HEBBLEWHITE, M. AND E. H. MERRILL. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377–387.

HEBBLEWHITE, M. AND E. H. MERRILL. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870.

HILL, M. 1975. Geology of the Sierra Nevada. University of California Press.

HOCKING, R. R. 1976. A Biometrics Invited Paper. The analysis and Seleciton fo Variables in Linear Regression. Biometrics 32:1–49.

HOSMER, D. W. J., S. LEMESHOW AND R. X. STURDIVANT. 2013. Applied Logistic Regression. John Wiley & Sons.

HULTHÉN, K. ET AL. 2015. Escaping peril: perceived predation risk affects migratory propensity. Biology Letters 11:20150466.

IGOTA, H. ET AL. 2004. Seasonal migration patterns of female sika deer in eastern Hokkaido, Japan. Ecological Research 19:169–178.

JOHNSON, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61:65–71.

JOHNSON, H. E., M. HEBBLEWHITE, T. R. STEPHENSON, D. W. GERMAN, B. M. PIERCE AND V. C. BLEICH. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

JOHNSON, H. E., L. S. MILLS, T. R. STEPHENSON AND J. D. WEHAUSEN. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

JONES, J. D., M. J. KAUFFMAN, K. L. MONTEITH, B. M. SCURLOCK, S. E. ALBEKE AND P. C. CROSS. 2014. Supplemental feeding alters migration of a temperate ungulate. Ecological Applications 24:1769–1779.

LOVARI, S., F. SACCONI AND G. TRIVELLINI. 2006. Do alternative strategies of space use occur in male Alpine chamois? Ethology Ecology & Evolution 18:221–231.

LUNDBERG, P. 1988. The evolution of partial migration in Birds. Trends in Ecology & Evolution 3:172–175.

MIDDLETON, A. D. ET AL. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

MILLER-RUSHING, A. J., T. T. HØYE, D. W. INOUYE AND E. POST. 2010. The effects of phenological mismatches on demography. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:3177–3186.

MILNER-GULLAND, E. J., J. M. FRYXELL AND A. R. E. SINCLAIR. 2011. Animal Migration: A Synthesis. OUP Oxford.

MONTEITH, K. L. ET AL. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:art47.

MORRISON, T. A. AND D. T. BOLGER. 2012. Wet season range fidelity in a tropical migratory ungulate. Journal of Animal Ecology 81:543–552.

MYSTERUD, A. 1999. Seasonal migration pattern and home range of roe deer (Capreolus capreolus) in an altitudinal gradient in southern Norway. Journal of Zoology 247:479–486.

MYSTERUD, A., L. E. LOE, B. ZIMMERMANN, R. BISCHOF, V. VEIBERG AND E. MEISINGSET. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos 120:1817–1825.

NELSON, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology 73:1069–1076.

PARMESAN, C. 2006. Ecological and evolutionary responses to recent climate change. Pp. 637–669 in Annual Review of Ecology Evolution and Systematics. Annual Reviews, Palo Alto.

PINHEIRO, J., D. BATES, S. DEBROY, D. SARKAR AND R CORE TEAM. 2015. “nlme”: linear and nonlinear mixed effects models. R, .

R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

ROBINSON, R. A. ET AL. 2009. Travelling through a warming world: climate change and migratory species. Endangered species research 7:87–99.

SCHLAEPFER, M. A., M. C. RUNGE AND P. W. SHERMAN. 2002. Ecological and evolutionary traps. Trends in Ecology & Evolution 17:474–480.

SEIP, D. R. AND F. L. BUNNELL. 1985. Foraging behaviour and food habits of Stone’s sheep. Canadian Journal of Zoology 63:1638–1646.

SINGH, N. J., L. BÖRGER, H. DETTKI, N. BUNNEFELD AND G. ERICSSON. 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecological Applications 22:2007–2020.

SINGH, N. J. AND G. ERICSSON. 2014. Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. Biology Letters 10:20140379.

SPITZ, D. 2015. “migrateR”: tools for animal movement classification.

U. S. FISH AND WILDLIFE SERVICE. 2007. Recovery plan for the Sierra Nevada bighorn sheep. U. S. Fish and Wildlife Service, Sacramento, California, USA.

VILLARET, J. C., R. BON AND A. RIVET. 1997. Sexual Segregation of Habitat by the Alpine Ibex in the French Alps. Journal of Mammalogy 78:1273–1281.

WEHAUSEN, J. D. AND R. R. RAMEY. 2000. Cranial morphometric and evolutionary relationships in the northern range of ovis canadensis. Journal of Mammalogy 81:145–161.

WHITE, K. S., N. L. BARTEN, S. CROUSE AND J. CROUSE. 2013. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

WHYTE, I. AND S. JOUBERT. 1988. Blue Wildebeest Population Trends in the Kruger National-Park and the Effects of Fencing. South African Journal of Wildlife Research 18:78–87.

WILCOVE, D. S. AND M. WIKELSKI. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.

ZENG, Z.-G. ET AL. 2010. Effects of plant phenology and solar radiation on seasonal movement of golden takin in the Qinling Mountains, China. Journal of Mammalogy 91:92–100.

TABLE 3-1. Opportunities to observe individual changes in migratory strategies among years in Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) 2006-2014. Instances in which an individual's strategy remained consistent are divided by strategy (“migrant to migrant” vs. “resident to resident”) These data only include sub-populations of Sierra Nevada bighorn sheep in which we observe both migrant and resident strategies. We observed 7 switches in strategy out of a possible 21 opportunities for a strategy-switching rate of 0.33 animals per year (SE = 0.12).

	Sub-populations			
Transition	Mt. Baxter	Sawmill Canyon	Mt. Langley	Mt. Warren
migrant to resident	2	1	1	0
migrant to migrant	2	6	4	0
resident to migrant	0	2	1	0
resident to resident	0	0	1	1

TABLE 3-2. Across-sub-population summary statistics of parameter estimates for migrant and resident Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). The mean, minimum, maximum, and standard error for each estimate is given. “γ” represents the estimated elevation of the resident or high-elevation migrant range. “δ” is the change in elevation between migratory ranges. “ρ” is the duration of residency on the winter range. “θ” and “θ_2” represent the midpoint of fall and spring migration, respectively. Similarly, “ψ” and “ψ_2” indicate the duration of fall and spring migratory movements (calculated as the time required to move from ½ to ¾ completion of the migratory movement).

	Term	**Units**	**Mean**	**Min.**	**Max.**	**Std. Error**	**Wald Stat.**
Mean Annual Elevation	(resident γ)	m	3465.77	3154.02	3942.98	180.86	0.05
Mean Summer Elevation	(γ)	m	3456.44	3134.48	3776.35	140.36	0.04
Altitudinal Movement	(δ)	m	-1211.66	-1783.89	-585.39	330.56	-0.27
Winter Range Residency	(ρ)	m	101.5	22.57	215.21	45.16	0.44
Timing of Fall Migration	(θ Fall)	days	58.96	1	157.08	40.31	0.68
Timing of Spring Migration	(θ Spring)	days	191.54	129.47	249.41	23.73	0.12
Duration of Fall Migration	(ψ Fall)	days	4.19	1	21	5.7	1.36
Duration of Spring Migration	(ψ Spring)	days	11.35	1	21	6.94	0.61

TABLE 3-3. Wald statistics for significant terms remaining in models of migratory tactics following backwards-stepwise selection. Population- and year-differences were both important in explaining differences in the vertical distance (δ), timing (θ) and duration of (ψ) migratory movements (see Eqn 2. for further details). Sub-populations are listed north to south and Mt. Baxter in 2011 was chosen as the reference category.

	Distance (δ)	**Timing (θ)**	**Duration (ψ)**
Mt. Warren	3.81	2.57	-0.94
Wheeler Ridge	2.57	2.89	-0.26
Sawmill Canyon	1.25	0.23	
Bubbs Creek	3.2	1.01	-1.41
Mt. Williamson	3.94	-1.41	-1.46
Mt. Langley	-0.45	1.16	-0.44
2005	-0.45		
2006	0.93	0.31	
2007	-2.96	-0.26	
2008	-2.09	0.99	
2009	-4.34	-0.21	1.01
2010	-2.05	-0.44	0.31
2013	0.57	-1.46	-0.21

FIGURE 3-1. Plot of elevation and Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) sub-populations in the eastern Sierra Nevada Mountains, California, USA. Sub-population boundaries shown are 95% kernel density estimates based on the location data included in our analysis. Sub-populations are listed in the legend from north to south. Even though they tend to be relatively small, most sub-populations include significant portions of high-elevation (above 4,000m, blue) and low-elevation (below 2,000m, white) terrain.

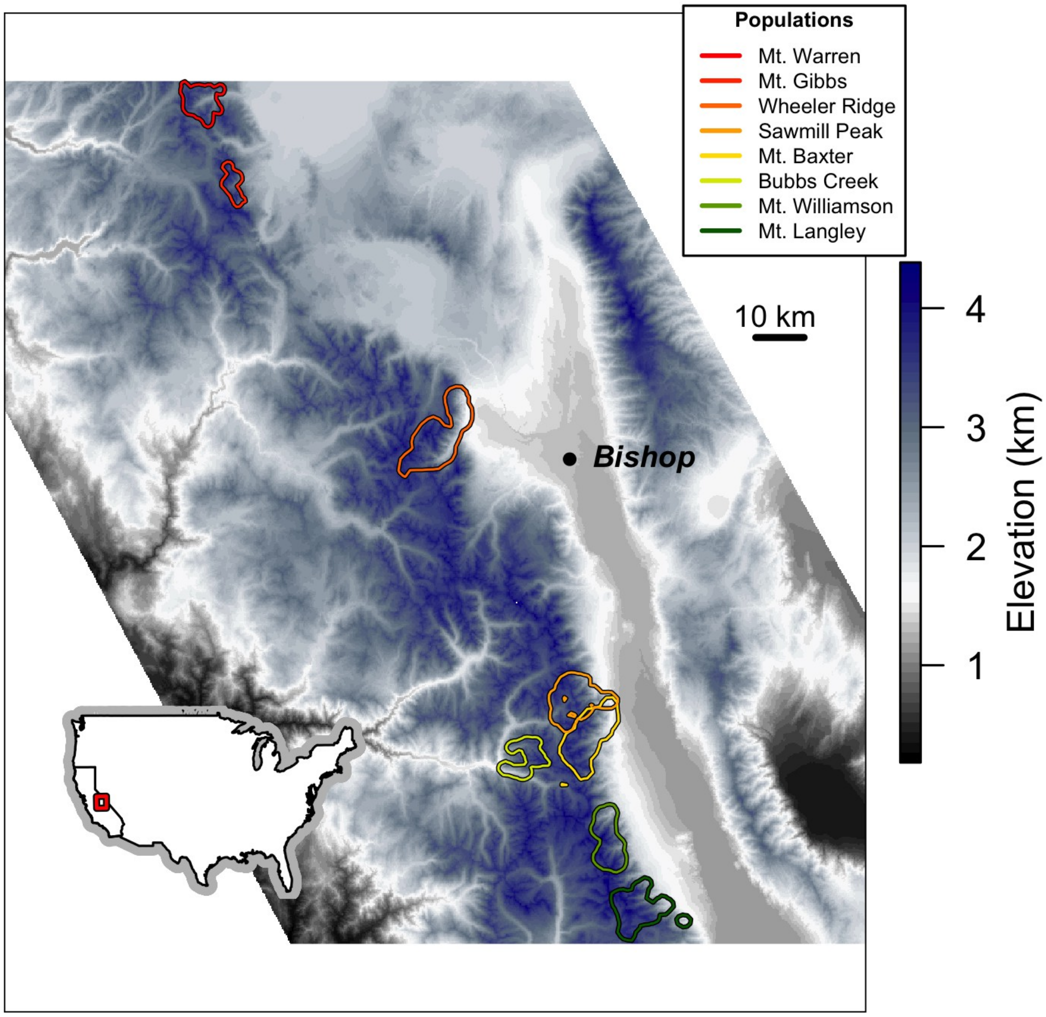


FIGURE 3-2. Example classification plots from two individual Sierra Nevada bighorn sheep (*Ovis Canadensis sierrae*) observed switching strategies between years. In 2007 we initially classified individual s110 as a migrant, but reclassified this movement as a resident foray based on failure to meet our minimum threshold for occupancy of the migratory range (21days, top left). Individual s265 in 2012 was also initially classified as migrant, but was reclassified as resident because estimated vertical separation between ranges did not meet our minimum threshold (500m, bottom left). Both of these individuals were classified as migrants in the year immediately following the resident classifications shown (two right panels).

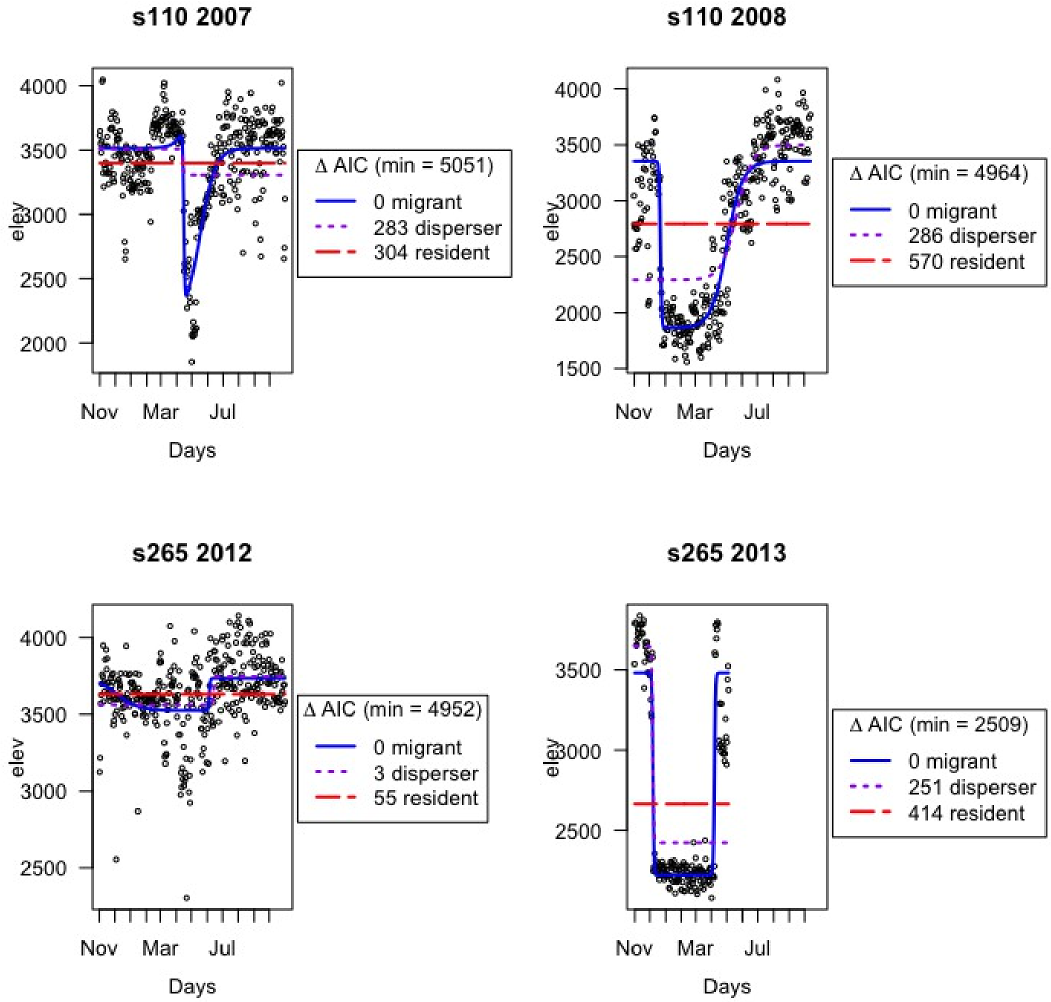


FIGURE 3-3. Migrant and resident classification of Sierra Nevada bighorn sheep (*Ovis canadensis* sierrae) by sub-population (ordered north to south). We observed both strategies in all but three of the sub-populations: Mt. Gibbs, Wheeler Ridge and Bubbs Creek (resident, migrant and migrant, respectively).

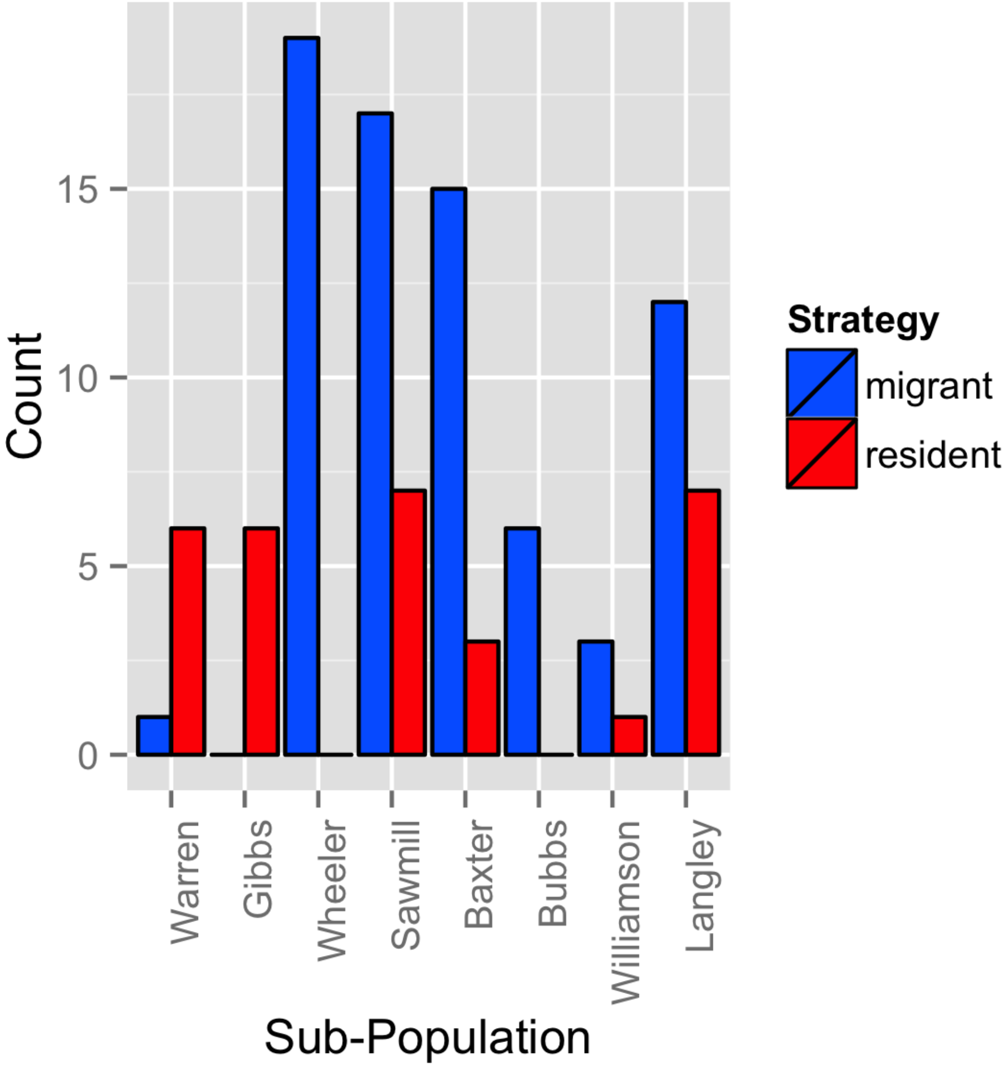
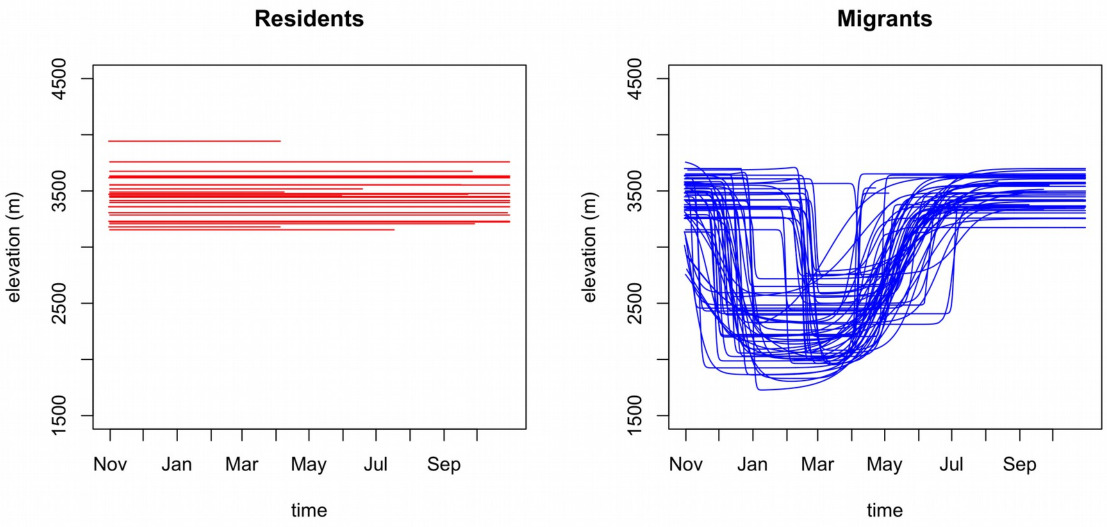


FIGURE 3-4. Combined plots of non-linear models fit to elevation for Sierra Nevada bighorn sheep (*Ovis canadensis* sierrae) migrant and resident animal-years, divided by migratory strategy. Line length (on x-axis) corresponds to date range of available data in each animal-year.



CHAPTER 4.

WHAT DO MIGRANTS DO DIFFERENTLY? QUANTIFYING STRATEGY-SPECIFIC DIFFERENCES IN RESOURCE USE AND SELECTION[3]

The idea that conditions affect individual fitness is fundamental to ecology (Grinnell 1917; Pulliam 2000; Soberón 2007). Through their behavior, mobile organisms have the luxury of altering the conditions they experience by changing their location in space (Johnson 1980; Lima and Dill 1990). Resource selection is a hierarchically nested process (Johnson 1980; Meyer and Thuiller 2006). Thus, strategies of resource selection often include changes in the strength and direction of selection as a function of spatial and temporal scale. This has been well documented in a wide array of species including elk (*Cervus elaphus*; Boyce et al. 2003), caribou (*Rangifer* tarandus; DeCesare et al. 2012) and grizzly bears (*Ursus arctor*; Ciarniello et al. 2007). The ability to select resources creates an opportunity for a single species to develop multiple behavioral strategies of resource use. Different behavioral strategies can carry different demographic consequences (Adriaensen and Dhondt 1990), making an understanding of these behavioral strategies crucial to linking observed distributions and demography (Morales et al. 2010).

In selecting resources, animals are often forced to balance the competing goals of acquiring energy and avoiding predation risk (Lima and Dill 1990; Houston et al. 1993).

---

[3] This chapter is formatted for submission to Ecography with Mark Hebblewhite and Thomas R. Stephenson as coauthors.

This balancing may manifest as a tradeoff between predation risk and nutritional access (Fryxell and Sinclair 1988; Hebblewhite and Merrill 2009) or between predation risk and other environmental factors limiting energy acquisition (Lima and Dill 1990). For example, areas with heavy snow often contain lower risk of predation, but deep snow decreases access to forage and increases the cost of locomotion and thermoregulation, thus reducing net energy gains (Telfer and Kelsall 1984; Nicholson et al. 1997; Dussault et al. 2005). Varying resource selection across multiple spatial scales provides a means of balancing these trade-offs (Senft et al. 1987). Selection at coarser scales has been hypothesized to be dominated by the primary factor limiting a species' distribution, with secondary limiting factors playing a more significant role at finer spatial scales (Senft et al. 1987; Rettie and Messier 2000; Dussault et al. 2005; White et al. 2013). For example, Rettie and Messier (2000) found support for the hierarchy hypothesis of resource limitation in resource selection by caribou, which was dominated by avoidance of wolves at the coarse scale, but best explained by forage at finer scales. Thus understanding a species' behavioral strategy (or strategies) requires integrating resource selection across these scales (DeCesare et al. 2012).

Migration is perhaps the most dramatic example of variation in behavioral strategies of resource use (Lack 1968; Boyce 1991; Griswold et al. 2010). Most migratory populations are now recognized to be partially migratory, displaying a range of strategies including both migration and residency (Cagnacci et al. 2011; Chapman et al. 2011). Here we focus on seasonal migration (hereafter simply “migration”), concerted periodic movement linked to seasonal changes in conditions between two or more distinct seasonal home ranges (Dingle and Drake 2007; Bunnefeld et al. 2011). Migratory behavior is common across a wide variety of species including every major vertebrate and many invertebrate taxa (Milner-Gulland et al. 2011). There is strong evidence that migratory populations are threatened and declining globally and many authors have suggested anthropogenic declines in resource availability as the culprit (Berger 2004; Wilcove and Wikelski 2008; Robinson et al. 2009). Through altering the conditions individuals experience, migratory strategies (migration and residency) are believed to increase their fitness either through a reduction in predation risk (predator avoidance hypothesis; Bergerud et al. 1990; Barten et al. 2001) or improved access to nutrition (e.g., the forage maturation hypothesis; Fryxell et al. 1988; Hebblewhite et al. 2008; and the competition avoidance hypothesis; Nelson 1995; Mysterud et al. 2011). Quantifying the differences between migrant and resident strategies represents a necessary first step toward developing a more mechanistic understanding of the consequences associated with migratory behavior. This connection between migratory behavior and resource use and selection remains poorly understood.

Partially-migratory and federally-endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae,* Sierra bighorn; U. S. Fish and Wildlife Service 2007) are one such species of conservation concern. While Sierra bighorn exhibit a single strategy of resource use in summer, sharing high-elevation alpine ranges, in winter some individuals migrate to low elevation ranges while others remain resident at high elevation (Chapter 2). Residents are exposed to severe winter conditions high in the Sierras, while in winter migration brings bighorn into increased contact with cougars, the species' main predator

(Johnson et al. 2012). Past work has hypothesized that bighorn sheep depend on spatial resources to reduce their risk of predation either by remaining at high elevation (where predators are less common) or remaining near rough terrain where their agility allows them to more easily avoid pursuit (Festa-Bianchet 1988). Thus migration and residency may represent alternative approaches to managing a forage-predation tradeoff. Previous attempts to understand resource selection in bighorn sheep have not distinguished between migrant and resident individuals and have largely focused on summer resource selection (Greene 2010; Johnson et al. 2012; Guisan et al. 2013). Winter resource selection by Sierra bighorn has only been examined at fine spatial scales (i.e. third-order—within individual home range; Greene 2010). However, nearly all adult mortality in this system occurs in winter, when migrants and residents are allopatric, emphasizing the importance of understanding differences in winter resource selection (CDFW unpublished data).

Resource selection functions (RSF; Boyce and McDonald 1999; Lele et al. 2013) can play an important role in informing conservation decisions, especially reintroductions and the identification of critical habitat (Guisan et al. 2013). To be useful to managers, these predictions must integrate selections across scale to provide a scale-independent measure of resource quality (DeCesare et al. 2012). More challenging, is the sensitivity of these models to assumptions about animal behavior. When more than one behavior is present in a population, failure to explicitly account for this difference has the potential to confuse inference. Research on resource selection in moose has shown that when behavioral differences are ignored the resulting predictions may represent an 'average' pattern of resource use which no individual follows (Gillingham and Parker 2008). Developing predictive models useful to management requires cross-scale integration of resource selection and explicitly accounting for differences in selection among different behaviors and across time.

Here we use RSFs in a hierarchical use-available design to quantify resource selection across three spatial scales, and integrate predictions across these scales by season (summer/winter) and winter status (migrant/resident) following DeCesare et al. (2012). We hypothesize that migrant and resident strategies in these populations represent contrasting scale-specific approaches to managing trade-offs between forage, predation risk and environmental conditions. More specifically, we hypothesize that migrants more strongly avoid predation risk at fine scales while showing stronger avoidance of snow and selection for forage at coarser scales, and residents avoid predation risk at coarser scales while avoiding snow and selecting forage at finer scales. Second, we also hypothesize that status-specific differences in winter resource selection exceed seasonal differences in selection by residents. Third, we hypothesize that across scales the combination of these status-specific differences in winter resource selection will translate to differences in patterns of use by migrants and residents such that migrants experienced increased access to forage but also increased use of terrain associated with predator avoidance while residents experienced harsher abiotic conditions (e.g. snow; Hebblewhite et al. 2008; Johnson et al. 2012). Finally, we hypothesize that spatial predictions of migrant and resident resource-selection will also explain sub-population differences in the propensity for migratory behavior.

Methods

Study Area

Sierra bighorn are endemic to the Sierra Nevada mountains, which form California's spine, extending 650km and varying in width from 75 to 125 km (Hill 1975). The southern half of this range displays tremendous relief, including peaks > 4250 m. The more gradual western slopes are cut by deep river drainages while the steep eastern face drops ~3000m to the valley below. Climate in summer (May-September) is relatively dry, with most annual precipitation arriving in winter (November-April) as snow. The range creates a strong rain shadow, resulting in open xeric vegetation on its eastern slopes. Low elevations (1250-2500m) typically support Great Basin bitterbrush-sage-brush scrub; mid elevations (2500-3300m) forests, pinyon-juniper woodland and subalpine meadows; and high-elevations (>3300m) sparse alpine vegetation with occasional meadows. Current and historical distribution of Sierra bighorn have been limited to the southern half of this range, which contains the bulk of the range's alpine habitat.

Location data

We outfitted female Sierra bighorn with global positioning system (GPS) collars (41 Tellus GPS collars, Followit; 50 Globalstar GPS collars, Northstar) following capture by helicopter net-gun (University of Montana IACUC AUP 046-11). Collars were deployed 2006 to 2013 and were programed to record ≥ 1 location per day at regularly scheduled intervals (2, 4 or 8 hours). We focused on the 8 largest populations, which represent more than 90% of all bighorn sheep in the subspecies (Figure 3-1). For this study and related monitoring objectives we analyze only data collected from females because of their importance in driving population dynamics (Eberhardt 2002; Johnson et al. 2010) and because sexual segregation is well documented in this species (Schroeder et al. 2010). GPS fix rates were high (>80%), indicating that risk of habitat induced bias is low (Frair et al. 2010).

Quantifying Migration

Sierra bighorn spend summers (June-October) in alpine habitat along the Sierra Nevada's crest, but display two distinct behavioral strategies in winter. While some individuals remain in the alpine year-round on high-elevation ranges (sometime > 4000m), most Sierra bighorn migrate to lower elevations (as low as 1500m) in early winter (November-January) where they typically remain until spring (April-May; Chapter 3). During winter residents take advantage of wind blown patches along the crest that remain relatively snow free, while migrants occupy xeric slopes at lower-elevation.

We resampled animal-years of data at one point per day and classified each as either migrant or resident using non-linear elevation-based modeling techniques adapted from Bunnefeld et al. (2011; Spitz 2015; Chapter 2; Chapter 3). We categorized individual migratory status using a set of a priori models each representing a different movement behavior (e.g. migration and residency) in which elevation varies as a function of time. We fit all models to each animal-year (defined November 1 – October 31) of location data and classified animal years based on AIC comparison of model performance (see Chapter 3 for details). Furthermore, we used the parameters estimated in these non-linear models to classify individual bighorn locations as belonging either to a summer, high-elevation winter (resident) or low-elevation winter (migrant) range. For animal-years classified as migrant, we identified all points between the midpoint of fall migration and the midpoint of spring migration as belonging to the migratory (winter) range and all other points as belonging to the summer range. For animal-years classified as resident, we identified all locations between the among-population mean dates of spring and fall migration as belonging to the resident (winter) range, and all other points as belonging to the summer range. In addition to quantitative rigor and a direct biological interpretation, this parameter-based approach to defining seasons has the added benefit of maximizing the amount of data we were able to include in our analyses. In contrast, past resource modeling work in migratory species has frequently excluded large portions of available data from seasonal analyses due to uncertainty surrounding a biologically relevant definition of season.

Resource Selection Function Modeling Framework

We consider three orders of selection in a use available design (following Meyer and Thuiller's 2006 update to Johnson 1980): S1, first order population-level selection of home ranges within the species range; S2, second-order individual-level selection of home ranges within population ranges; and S3, third-order individual-level selection of locations within individual ranges (Figure 4-1). Following DeCesare et al (2012) we sampled used and available locations in a hierarchical manner to take advantage of the conditional nesting of these three orders of selection. This allowed us to generate scale-independent estimates of the relative probability of use for a given pixel. We estimated SRSFs for each status-season following DeCesare et al (2012):

$$\begin{aligned} w_{\mathrm{SRSF}} &= P(S1, S2, S3) \\ &= P(S1) \times P(S2|S1) \times P(S3|S2) \\ &= P(S1) \times P(S2) \times P(S3). \qquad \text{Eqn. 4-1.} \end{aligned}$$

where Wsrsf is the integrated relative probability of use, P(S1, S2, S3) is the relative probability of selecting a location at the first, second and third orders, P(S2|S1) is the relative probability of second order selection given first order selection and P(S3|S2) is the relative probability of third order selection given second order selection. We quantified S1 selection by treating population ranges as use and the species range as available. For each population we randomly selected a number of used locations equal to the average number of locations per population (Figure 4-1). To quantify S2 selection we treated population ranges as available and individual home ranges as use (Figure 4-1). For each individual range we randomly sampled a number of use locations equal to the average number of locations per animal-year. We sampled S3 selection by considering individual home ranges as available and recorded animal locations as use (Figure 4-1). To adequately characterize the increased variability of available locations, at each of these scales we randomly selected four times as many used points as available (Manly et al. 2002; Johnson and Gillingham 2008).

We defined the species range as all continuous locations that are: 1) above 1,370m in elevation; and 2) within 1.5km of escape terrain (defined as having a slope greater than 30 degrees; “Study Area” in Figure 4-1). To limit the influence of outlying points, we defined population ranges as the union of 95% fixed-kernel isopleth for summer, resident and migrant points by population, which we clipped by the species range (calculated using the reference bandwidth, Worton 1989; Figure 4-1). We calculated individual home ranges in a similar manner, calculating the union of 95% isopleths for summer, and resident or migrant points by animal-year and clipping the resulting polygon by the population-level range. To maintain consistency in hierarchical sampling, we also excluded by animal-year all used locations falling outside of the individual range.

Resource Variables

We selected candidate variables based on past work modeling resource selection in bighorn sheep, but also included three novel covariates relevant to winter resource use (Bleich et al. 2008; Greene et al. 2012; Guisan et al. 2013). Variables of previously demonstrated importance included elevation (m), slope (degrees), vector ruggedness measure (VRM, higher values indicating greater ruggedness; Sappington et al. 2007), solar radiation index (SRI, higher values indicating greater received solar energy; Keating et al. 2007), escape terrain (categorical—was slope greater than 30 degrees; Bleich et al. 2008) and distance to escape terrain (m). We included the presence of trees to account for visibility and selection for Normalized Difference Vegetation Index (NDVI), both of which are of known importance to bighorn (Bleich et al. 2008). The three novel winter-specific covariates we included were an index of winter snow cover, an index of winter plant productivity and an index of the size of snow free patches. We excluded covariates that were correlated ($R^2 \geq 0.7$) and those with variance inflation factors > 10 separately at each of the three spatial scales considered (Montgomery et al. 2012). All covariates were measured at a 30m scale. To facilitate model fitting and facilitate the comparison of model parameters, we centered and standardized each covariate by subtracting the mean and dividing by two times the standard deviation (Gelman 2008).

Normalized Difference Vegetation Index (NDVI) and fractional snow cover provide important information describing the severity and consistency of winter conditions. NDVI provides an index of plant productivity (and thus available nutrition, Pettorelli et al. 2005; Greene et al. 2012), while snow cover is known to impose additional costs on ungulates (e.g. by impeding locomotion, increasing thermoregulatory demands and limiting availability of food, Telfer and Kelsall 1984). To create an index of plant nutrition available in winter we averaged NDVI values derived from LANDSAT 7 images in winter months (January 1- April 1) over an eleven-year span (2000-2011) after censoring pixels in which fractional snow cover met or exceeded 0.10. We also created an index of winter snow cover following an analogous approach, taking per-pixel averages of fractional snow cover (Rittger et al. 2013) from LANDSAT 7 images in winter months (January 1- April 1) over the same 11-year period. Thus, higher mean NDVI values should represent higher winter forage quality, while higher mean fractional snow values should represent increased snow cover. We interpret these NDVI values as an index of forage quality measuring the persistence of plant growth from the prior growing season through the winter.

We next used our index of winter snow cover as the basis for an index of snow free patch size, which acts as an index of connectivity, given that snow can act as a barrier to bighorn movement (Telfer and Kelsall 1984; Goodson et al. 1991). To estimate snow-free patch size at a relevant scale, we calculated the total number of pixels in a moving window that fell below some threshold, such that higher values would represent patches with less snow. We compared combination of window size (3, 5 and 7 pixels) and cutoff (0.2, 0. .4, 0.6) to our other covariates at each scale, excluding cutoff-window combinations correlated with another variable ($R^2 \geq 0.7$). We then performed a univariate comparison of the remaining combinations, choosing the window-cutoff combination with the greatest predictive ability at the third-order (5 pixel window, 0.4 threshold).

Data Analysis

We estimated resource selection functions across all three scales following Manly et al. (2002) using the exponential approximation to the logistic discriminant function which yields a relative probability of use (see Lele et al. 2013; McDonald 2013):

$$w(x) = \mathrm{e}^{(B_1 * x_1 + \ldots + \mathrm{B}_i * x_i)} \qquad \text{Eqn. 4-2}$$

and rescaled predicted values between 0 and 1 using a linear stretch (Johnson et al. 2004):

$$\mathrm{w} = \frac{w(x) - w_{\min}}{w_{\max} - w_{\min}} \qquad \text{Eqn. 4-3}$$

Our modeling strategy involved starting with the most complex model and sequentially removing non-significant terms (Harrell 2013). We considered only a limited number of biologically-meaningful interactions (discussed below; Hosmer et al. 2013). We included quadratic terms to allow for non-linear selection of NDVI, slope and elevation. These covariates are of known importance to bighorn, but the cost of their use is expected to increase at extreme values, leading to selection for intermediate values (Bleich et al. 2008). For example bighorn may select steep slopes as part of a strategy of predator avoidance, but may also avoid the steepest slopes because these limit movement.

At the first order we fit two models. We fit a naive model:

$$w(x) = e^{\left(B_1 * x_1 + B_{1s} * x_1 * \text{summer} + \ldots + \mathrm{B}_i * x_i + B_{is} * x_i * \text{summer}\right)} \qquad \text{Eqn. 4-4}$$

which assumes winter selection is consistent across migrants and residents, but allows selection to differ by season (summer). For each covariate we tested an interaction with the categorical variable “summer” to directly estimate the magnitude and direction of seasonal differences in resource selection. We then also fit a behavioral model testing each covariate for interactions with season (summer) and status (migrant), i.e.

$$w(x) = e^{\left(B_1 * x_1 + B_{1m} * x_1 * \text{migrant} + B_{1s} * x_1 * \text{summer} + \ldots + \mathrm{B}_i * x_i + B_{im} * x_i * \text{migrant} + B_{is} * x_i * \text{summer}\right)} \qquad \text{Eqn. 4-5}$$

The interactions we included were constructed so that base predictions refer to resident selection in winter. Thus, with the $B_{1m} * x_1 * \text{migrant}$ interaction as an example, if the B_{1m} term is found significant, we can interpret this term as evidence for status-specific difference in resource selection by Sierra bighorn, with the magnitude of the B_{1m} term indicating the size of the difference in selection between migrants and residents.

At each subsequent scale we tested a naive (winter) model and separate models for summer, resident and migrant selection, which we refined through backwards-stepwise regression (Harrell 2013). At the second and third order, all of our staring models included the same set of covariates. We contend that our winter-specific covariates (snow-cover index, vegetation index and snow-free patch size) are still biologically relevant in summer, though their interpretation is reversed in this season, i.e. locations with snow in winter offer improved growing conditions in summer (Kudo 1991), while locations allowing winter growth are likely more xeric in warmer months (Mårell et al. 2006). Population was treated throughout as a random effect as was individual at the second and third-orders to account for population and individual level differences in selection (Gillies et al. 2006). We randomly withheld approximately 20 percent of animal-years by population and season from the model training for later use as external validation (n = 16, see next section).

Validation

We validated our models using k-folds cross validation separately for integrated predications and each of the three constituent scales (Boyce et al. 2002). To test model fit to the training data, models were validated using internal resubstituted data used in model fitting. To test the models' predictive performance, we also validated each model using an external data set withheld from the model fitting process. To better compare performance of the behavioral and naive models, we validated naive model predictions for migrant and resident locations separately. Predictions for mapping and model validation were based on model averages (i.e. ignored random effects) and excluded any coefficients whose confidence intervals overlapped zero. We used t-tests to compare Spearman rank correlation values from naive and behavioral models. To compare whether resident predictions were closer to summer or migrant predictions, we again employed k-folds cross validation, validating migrant and summer predictions using only winter resident locations. We compared the resulting Spearman rank correlation values using t-tests.

Migratory Propensity

We tested the ability of spatial RSF predictions to predict population differences by estimating the percent of each population that was suitable for migrant and resident strategies and then using these estimates to fit an a priori set of models using beta regression, a regression model appropriate for the analysis of proportion data (Ferrari and Cribari-Neto 2004). We relied on previous analyses (Chapter 3) to determine the propensity for migratory behavior in each of the 8 populations represented in the data used to fit our resource selection models. We adjusted estimates of migratory propensity equalling 1 or 0 by an arbitrarily small amount (0.01) to represent our uncertainty in these estimates truly representing single-status populations and to meet the requirements for beta regression (Ferrari and Cribari-Neto 2004). To estimate the amount of each population range (defined above) suitable to a specific migratory status, we calculated the mean value of used points for each status-scale combination and then sampled 10,000 random points from each population and counted the number of points that had predicted values exceeding this threshold (Liu et al. 2005). We estimated the percent of each population suitable as well as the percent of each population suitable for both s(e.g. Figure 4-2).We repeated this for each spatial scale (first, second and third order) and for integrated predictions using as our cutoff the mean integrated prediction of used third-order locations. Our a priori model set included terms for the percent of pixels exclusive to each status, total for each status and shared by both migrants and residents. We compared this model set using AIC (Burnham and Anderson 2002). All analyses were performed in Program R (R Core Team 2014) using the betareg, lme4, migrateR, raster, and rgdal packages (Cribari-Neto, Francisco and Zeileis 2010; Bates, et al. 2014; Bivand et al. 2014; Hijmans and van Etten 2014; Spitz 2015).

Results

The first-order behavioral model (accounting for both migratory status and season) outperformed the naive season-only model. Comparison of first-order models assigned behavioral and naive models $AIC_{weights}$ of 1 and 0 respectively (Table 4-1). Selection for covariates showed significant differences by migratory status and scale. Among covariates included in migrant, resident and naive winter models, the magnitude and direction of parameter estimates differed within models at the same scale. The importance and inclusion of covariates varied by model and scale (Table 4-2). Among first order models, the sign of parameter estimates were consistent, but magnitudes varied (Table 4-2). All first-order selection was dominated by avoidance of fractional snow cover, avoidance of intermediate elevation and avoidance of intermediate NDVI values. Individuals selected locations close to escape terrain, avoiding trees, areas of high solar radiation and large snow-free patches. Migrant and naive winter models showed selection for steeper slopes, while residents showed selection for intermediate slopes. Finally, selection for NDVI increased in escape terrain in the migrant and naive models, while selection for NDVI increased with distance from escape terrain in resident and naive models. Migrant models showed no relationship between NDVI and fractional snow cover or distance to escape terrain, but resident and naive models showed increasing and decreasing selection of NDVI with distance from escape terrain and fractional snow cover, respectively.

All second-order models included strong selection for proximity to escape terrain and showed weaker avoidance of trees, avoidance of large snow-free patches and selection of intermediate NDVI values. Migrant and resident selection at this scale differed in sign for several resource covariates. In these cases the naive models tended to show weak selection or avoidance, intermediate to the opposing selection found in behavioral models. At the second Sierra bighorn migrants and residents showed opposing selection for elevation, fractional snow cover and slope, with migrants selecting intermediate elevation, avoiding fractional snow cover and selecting steeper slopes (Table 4-2, Figure 4-3). In contrast, resident Sierra bighorn selected higher elevations, higher snow cover and flatter terrain (Table 4-1, Figure 4-3). Migrant and naive models stressed the importance of Sierra bighorn selecting for solar radiation, while selection by residents was inconsequential (Table 4-2). Conversely, resident and naive model included strong evidence for Sierra bighorn more strongly avoiding snow covered areas that also receive strong solar radiation, while this interaction was only moderately important to selection by migrants (Table 4-2). The naive model showed increased avoidance of trees as distance from escape terrain increased-- a pattern of selection seen neither in the resident nor in the migrant model. Migrant and naive models also showed higher NDVI values in trees, while resident models did not. Resident and naive selection for slope decreased with increasing elevation, while migrant selection for slope remained independent of elevation (Table 4-2).

Third-order models showed that Sierra bighorn consistently avoided fractional snow cover, selected rugged terrain, selected intermediate NDVI values, selected steep slopes more strongly at lower elevation, and showed stronger avoidance of trees as distance to escape terrain increased (Table 4-2). Although all models predicted avoidance of snow, this was far less important to migrant selection ($|z| < 15$; Table 4-2) than to resident, naive or summer selection ($|z| > 30$). Similarly, all models showed weakened selection for NDVI with increasing winter snow cover, but this relationship was weaker for migrant ($|z| < 4$; Table 4-2) than for resident, naive or summer selection ($|z| > 14$). Third-order models showed opposing migrant and resident Sierra bighorn selection for snow-free patch size and solar radiation index, with migrants selecting for snow-free areas, high solar-radiation while residents strongly avoided larger snow-free areas and weakly avoided solar radiation (Figure 4-3). Third order models also showed contrasting migrant and resident selection for slope, where residents selected for intermediate slopes (approximately 20-50 degrees, Figure 4-3) while resident selection for slope was nearly flat.

Integrated migrant and resident models validated well across all three scales. Internal validation of models using resubstituted training data showed strong predictive capacity of single-scale models both at the scale models were developed (mean Spearman rank correlation, $\rho = 0.974$) and across other extents ($\rho = 0.986$; Table 4-3). Scale integrated models validated well across all three extents ($\rho = 0.965$). Our external validation of S2 and S3 models showed a similar pattern (Table 4-4). When evaluated with an independent data set of animal-years withheld from model fitting, models performed comparably to internal validation, with scale-specific showing slightly lower and scale-integrated models slightly higher performance ($\rho = 0.977$ and 0.97, respectively). We found no difference in performance between predictions from behavioral and naive integrated models (internal: $t_2 = -1.59$, $p = 0.25$; external: $t_1 = 0.36$, $p = 0.78$). We were unable to find any difference in validation of migrant and summer predictions with resident locations ($t = 0.71$, $p = 0.51$; Table 4-5). Thus seasonal- and status-specific differences in selection appeared equivalent in their predictive importance.

Winter used-locations showed significant differences between conditions experienced by migrants and residents. At the first-order, migrants used locations at lower elevations with less snow, larger snow free patches, higher NDVI slightly steeper slopes and slightly more rugged terrain (Table 4-6). There was no difference in use of aspect and distance to escape terrain between migrants and resident at the first order. At the second order, migrants and residents again differed chiefly in elevation and fractional snow cover, followed by NDVI, slope, and snow-free patch size with only slight differences in distance to escape terrain and vector ruggedness measure. There were no detectable differences in aspect and SRI. Differences in use were largest at the third-order scale and the magnitude of differences followed a similar pattern as at coarser scales. Differences in elevation, snow-free patch size and fractional snow cover were approximately double the magnitude of differences seen at the first and second order. Migrants used locations with higher NDVI, higher SRI and steeper slopes. Compared to residents, migrants used locations closer to escape terrain.

Model predictions strongly predicted among population differences in the propensity for migratory behavior. Correlation among status-specific predictions at different scales ($R^2 > 0.7$) prevented us from including predictions from more than one scale in a single model. At every scale the top model included only a single term for the percent of migrant habitat predicted (Table 4-7). At the second- and third-order, the total percent of area suitable for migrants was the best predictor, while at the integrated and first order scales the percent of area suitable for migrants exclusively (i.e. after subtracting the percent of area predicted to be suitable to both strategies) was the best predictor. First order predictions of the proportion of migrant habitat performed slightly better than migrant integrated predictions (ΔAICc = 0.83), with second and third order migrant predictions showing similar but slightly poorer performance (Table 4-7). First order predictions of the proportion of migrant habitat and population-level migratory propensity were strongly correlated ($R^2 = 0.80$).

Discussion

Our results affirm the presence of scale-specific differences in winter resource selection by migrants and residents. Status-specific differences in resource selection offered contrasting solutions to a classic forage-predation tradeoff. Lower elevations have better winter forage, but earlier work has shown that these areas carry an increased risk of predation by cougar (*Puma concolor*), Sierra bighorn's primary predator. Residents avoided predation risk at the coarsest scale, but focused on forage in fine-scale selection, whereas migrants selected for forage at the coarsest spatial scale, but displayed fine scale selection dominated by the avoidance of predation risk. Integrated across scales, these inverse patterns of selection resulted in similar overall patterns of selection and seasonal distribution. In spite of these similarities, we observed status-specific differences in resource use with migrants gaining better access to forage. These differences support our hypothesis that migrants and residents contrast in their response to trade-offs between environmental conditions, forage and predation risk. Consistent with previous work on alpine ungulates, snow, forage and “safe” terrain features were important to resource selection across the three scales we examined (Festa-Bianchet 1988; Mysterud et al. 1999; DeCesare and Pletscher 2006; Walker et al. 2007; Zweifel-Schielly et al. 2009; Greene 2010).

Winter resource selection by migrants and residents, however, did not conform directly to our predictions, instead displaying more complex relationships as a function of scale. For example, contrary to our predictions, migrants and residents showed consistent coarse scale avoidance of snow. Following the hierarchy hypothesis of resource limitation (Rettie and Messier 2000) we suggest that snow is among the most important factors limiting both migrant and resident Sierra bighorn in winter. Snow simultaneously increases the energetic demands of locomotion and impairs access to forage (Telfer and Kelsall 1984; Goodson et al. 1991). Consistent with our predictions, compared to migrants, residents showed stronger selection for proximity to escape terrain at coarse scales. Migrants, however, showed stronger first-order selection for escape terrain than did residents and at the third order residents actually avoided escape terrain. In contrast, migrants showed strong third-order selection for escape terrain despite second-order indifference. Thus, migrants showed fine-scale behavioral differences from residents which may help to mitigate the increased exposure to predation risk they experience after migrating to lower elevations. These findings support the hierarchy hypothesis of resource limitation, suggesting that migrants in this system are most limited by the availability of forage, whereas residents are most limited by predation.

We failed to find support for our second hypothesis, that status-specific differences in winter resource selection exceeded the seasonal difference in resource selection by residents in winter and summer. Instead, we found that status-specific and seasonal differences in resource selection were similar in magnitude. Although the importance of accounting for seasonal differences in selection is well appreciated (Boyce and McDonald 1999; Boyce et al. 2002; Manly et al. 2002), our results stress that in migratory systems accounting for status-specific differences can be equally important.

Our results also supported our third hypothesis; compared to migrants, residents on average occupied snowier conditions, and had less access to vegetation even though they appeared less tied to escape terrain. Migratory status in Sierra bighorn thus appears to represent a classic forage-predation trade-off in which migrants prioritize access to nutrition at the expense of increasing their risk of predation, while residents prioritize predator avoidance at the expense of nutritional intake and increased energetic demands (Nicholson et al. 1997; Hebblewhite and Merrill 2009; White et al. 2013). It is worth noting that Sierra bighorn provide an unusual example, contrary to the bulk of the literature, in at least two important and related respects. First, Sierra bighorn are not expected to experience increased predation risk while migrating. In other ungulates, migrants experience elevated predation risk during their migratory movements, which has been explained by decreased familiarity with the areas they traverse (Nicholson et al. 1997; Hebblewhite and Merrill 2007). In contrast, Sierra bighorn move short distances (along a steep altitudinal gradient, Chapter 3) and are not expected to overlap with predators until arriving on their migratory range (Johnson et al. 2012). Consequently a second difference is that unlike most migrants Sierra bighorn migrants move toward an area of higher predation risk, measured by predator density, rather than avoiding it (Hebblewhite and Merrill 2009; Johnson et al. 2012; Avgar et al. 2014). This explains the differences in our findings from other studies that have shown migrants to be more sensitive to predators at fine, rather than at coarse scales (Hebblewhite and Merrill 2009). Despite these differences, the outcome measured in use appears to be the same for Sierra bighorn as with residents in other systems: residents pay for avoiding predation risk with lower forage quality. An individual's reproductive history is therefore likely to play a pivotal role in determining her migratory status, with the nutritional stress of lactation leading females with young to accept the added risks of migration (see Chapter 5).

The predictions from our spatial models provide an initial basis for prioritizing areas of conservation concern, or other management actions including, as in the case of Sierra bighorn, reintroductions (Guisan et al. 2013). Our scale-integrated status-specific models clearly organize this information across three scales in a way that can be easily interpreted and applied to management decisions (DeCesare et al. 2012). Models accounting for migration revealed opposing selection by migrants and residents that was obscured or omitted in models ignoring migratory status. Thus accounting for migration yielded additional insight into a range of scale-specific behavioral differences attendant on migratory strategy. These results echo resource selection work in moose, where models averaging selection across individuals were shown to correspond to conditions that no individual selected (Gillingham and Parker 2008). Like Gillingham and Parker (2008), our behavioral models provide additional insight into the ecology of our system that would have been masked had we ignored differences in migratory strategy. A further example of the value of our strategy-specific predictions is that they currently provide the only available method for estimating population-level prevalence of migratory behavior. If migrant and resident demography differ, estimating the prevalence of these strategies in new herds could be key to successful reintroductions. For example, even if residents made greater per-capita contributions to population growth (Chapter 5), in most systems migrants outnumber residents and may thus represent a greater net contribution to population growth (Fryxell et al. 1988). Partially migratory populations are thus likely to be larger and more resilient to perturbation than all-migrant or all-resident groups.

Despite this ability to predict population-level behavior, the extent to which accounting for migration improved our spatial predictions remains somewhat ambiguous. While model selection criteria clearly favored models that accounted for migratory behavior, model validation failed to reveal a detectable difference in the performance of behavioral and naive models, both with internal or external data sets. One possible explanation for the difficulty of detecting differences in predictive performance between behavioral and naive models is that within strategy opposing selection across different scales effectively “canceled out” in much the same way as opposing selection between migrants and residents dropped out of naive single scale models. Thus although the naive model validated well, it masked the behavior differences that separate migrants and residents and should be treated with caution. We argue that the ecological insight our biological models provide outweigh their added cost in computational complexity. Particularly for management applications requiring extrapolation (e.g. reintroductions, Guisan et al. 2013), we encourage consideration of models with a stronger biological basis, even in cases where simpler models have equivalent predictive performance.

Differences in selection among years or sub-populations could also limit our ability to detect differences in performance between behavioral and naive models. Although we expect migratory and resident behavior to vary both by sub-population and year, the computational expense of accounting for migratory strategy prevented us from including these sources of variation in our analysis. Johnson et al (2012) found evidence among subpopulations and within years showing that Sierra bighorn sub-populations facing greater predation risk selected safer terrain than did populations at lower risk, but that risk aversion in Sierra sheep decreased as winter progressed, presumably as a result of accumulated nutritional stress. Greene (2010) found evidence of behavioral responses across years, demonstrating changes in selection as a function of predation risk across two winters for two Sierra bighorn subpopulations (Mt. Baxter and Sawmill Canyon). While we expect these differences in selection to be smaller than those observed between strategies, simultaneously accounting for interannual and inter-population differences in selection may hold the key to resolving the contrast between migrant and resident behavior.

Perhaps most importantly, the criteria through which the behavioral model distinguishes migrant and resident resource selection provide a promising basis for further advancing our understanding of the costs and consequences associated with migratory behavior. The demographic consequences of space use remain a major gap in our understanding of migratory populations (Morales et al. 2010). Although researchers often find it convenient to assume that migrants and residents have equivalent fitness (i.e. that migration constitutes an evolutionary stable strategy; Lundberg 1988; Kaitala et al. 1993; Griswold et al. 2010), it is important to remember that this need not be the case; partial migration can be maintained as a conditional strategy even when one strategy is leads to far lower fitness (Lundberg 1988). Andriaensen and Dhondt (1990) were able to demonstrate that for European Robins (*Erithacus rubecula*), migration was a conditional strategy in which individuals made the best of a bad case. In this system, resident males had the highest reproductive success, but only males in top physical condition were able to survive the energetic demands of winter at higher latitudes (Adriaensen and Dhondt 1990). Thus, migrating males benefited from a relative increase in fitness; although their reproductive success remained lower than residents, it was higher than the near certain death attendant on attempted residency by poorer-condition individuals. Sierra bighorn's high plasticity in choice of migratory strategy (Chapter 3) raises the important possibility that residency in this system may be a state-dependent strategy, i.e. that only individuals entering winter in top body condition have sufficient energetic reserves to weather the increased energetic demands and decreased nutritional intake attendant on residency

(Chapter 5).

Literature Cited

ADRIAENSEN, F. AND A. A. DHONDT. 1990. Population-Dynamics and Partial Migration of the European Robin (Erithacus rubecula) in Different Habitats. Journal of Animal Ecology 59:1077–1090.

AVGAR, T., G. STREET AND J. M. FRYXELL. 2014. On the adaptive benefits of mammal migration. Canadian Journal of Zoology 92:481–490.

BARTEN, N. L., R. T. BOWYER AND K. J. JENKINS. 2001. Habitat use by female caribou: Tradeoffs associated with parturition. Journal of Wildlife Management 65:77–92.

BATES, D., M. MAECHLER, B. BOLKER AND S. WALKER. 2014. Linear Mixed-Effects Models Using Eigen and S4. R, .

BERGER, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–321.

BERGERUD, A. T., R. FERGUSON AND H. E. BUTLER. 1990. Spring migration and dispersion of woodland caribou at calving. Animal Behaviour 39:360–368.

BIVAND, R., T. KEITT AND B. ROWLINGSON. 2014. Bindings for the Geospatial Data Abstraction Library. R, .

BLEICH, V. C., H. E. JOHNSON, S. A. HOLL, L. KONDE, S. G. TORRES AND P. R. KRAUSMAN. 2008. Fire History in a Chaparral Ecosystem: Implications for Conservation of a Native Ungulate. Rangeland Ecology & Management 61:571–579.

BOYCE, M. 1991. Migratory Behavior and Management of Elk (cervus-Elaphus). Applied Animal Behaviour Science 29:239–250.

BOYCE, M. S. ET AL. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. Ecoscience 10:421–431.

BOYCE, M. S. AND L. L. MCDONALD. 1999. Relating populations to habitats using resource selection functions. Trends in Ecology & Evolution 14:268–272.

BOYCE, M. S., P. R. VERNIER, S. E. NIELSEN AND F. K. A. SCHMIEGELOW. 2002. Evaluating resource selection functions. Ecological Modelling 157:281–300.

BUNNEFELD, N. ET AL. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

BURNHAM, K. P. AND D. R. ANDERSON. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

CAGNACCI, F. ET AL. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

CHAPMAN, B. B., C. BRÖNMARK, J.-Å. NILSSON AND L.-A. HANSSON. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

CIARNIELLO, L. M., M. S. BOYCE, D. R. SEIP AND D. C. HEARD. 2007. Grizzly bear habitat selection is scale dependent. Ecological Applications 17:1424–1440.

CRIBARI-NETO, FRANCISCO AND A. ZEILEIS. 2010. Beta Regression in R. Journal of Statistical Software 34.

DECESARE, N. J. ET AL. 2012. Transcending scale dependence in identifying habitat with resource selection functions. Ecological Applications 22:1068–1083.

DECESARE, N. J. AND D. H. PLETSCHER. 2006. Movements, Connectivity, and Resource Selection of Rocky Mountain Bighorn Sheep. Journal of Mammalogy 87:531–538.

DINGLE, H. AND V. A. DRAKE. 2007. What Is Migration? BioScience 57:113–121.

DUSSAULT, C., J.-P. OUELLET, R. COURTOIS, J. HUOT, L. BRETON AND H. JOLICOEUR. 2005. Linking moose habitat selection to limiting factors. Ecography 28:619–628.

EBERHARDT, L. L. 2002. A paradigm for population analysis of long-lived vertebrates. Ecology 83:2841–2854.

FERRARI, S. L. AND F. CRIBARI-NETO. 2004. Beta Regression for Modelling Rates and Proportions. Journal of Applied Statistics 31:799–815.

FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586.

FRAIR, J. L., J. FIEBERG, M. HEBBLEWHITE, F. CAGNACCI, N. J. DECESARE AND L. PEDROTTI. 2010. Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. Philosophical Transactions of the Royal Society of London B: Biological Sciences 365:2187–2200.

FRYXELL, J., J. GREEVER AND A. SINCLAIR. 1988. Why Are Migratory Ungulates so Abundant. American Naturalist 131:781–798.

FRYXELL, J. M. AND A. R. E. SINCLAIR. 1988. Causes and consequences of migration by large herbivores. Trends in Ecology & Evolution 3:237–241.

GELMAN, A. 2008. Scaling regression inputs by dividing by two standard deviations. Statistics in Medicine 27:2865–2873.

GILLIES, C. S. ET AL. 2006. Application of random effects to the study of resource selection by animals. Journal of Animal Ecology 75:887–898.

GILLINGHAM, M. P. AND K. L. PARKER. 2008. The Importance of Individual Variation in Defining Habitat Selection by Moose in Northern British Columbia. Alces 44:7–20.

GOODSON, N., D. STEVENS AND J. BAILEY. 1991. Effects of Snow on Foraging Ecology and Nutrition of Bighorn Sheep. Journal of Wildlife Management 55:214–222.

GREENE, L. 2010. Short-term effects of wildfire on Sierra Nevada bighorn sheep habitat ecology.

GREENE, L., M. HEBBLEWHITE AND T. R. STEPHENSON. 2012. Short-term vegetation response to wildfire in the eastern Sierra Nevada: Implications for recovering an endangered ungulate. Journal of Arid Environments 87:118–128.

GRINNELL, J. 1917. The Niche-Relationships of the California Thrasher. The Auk 34:427–433.

GRISWOLD, C. K., C. M. TAYLOR AND D. R. NORRIS. 2010. The evolution of migration in a seasonal environment. Proceedings of the Royal Society B: Biological Sciences 277:2711–2720.

GUISAN, A. ET AL. 2013. Predicting species distributions for conservation decisions. Ecology Letters 16:1424–1435.

HARRELL, F. E. 2013. Regression Modeling Strategies: With Applications to Linear Models, Logistic Regression, and Survival Analysis. Springer Science & Business Media.

HEBBLEWHITE, M. AND E. H. MERRILL. 2007. Multiscale wolf predation risk for elk: does migration reduce risk? Oecologia 152:377–387.

HEBBLEWHITE, M. AND E. H. MERRILL. 2009. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. Ecology 90:3445–3454.

HEBBLEWHITE, M., E. MERRILL AND G. MCDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population.

Ecological Monographs 78:141–166.

HIJMANS, R. J. AND J. VAN ETTEN. 2014. Raster: Geographic Analysis and Modeling with Raster Data. R, .

HILL, M. 1975. Geology of the Sierra Nevada. University of California Press.

HOSMER, D. W. J., S. LEMESHOW AND R. X. STURDIVANT. 2013. Applied Logistic Regression. John Wiley & Sons.

HOUSTON, A. I., J. M. MCNAMARA AND J. M. C. HUTCHINSON. 1993. General Results concerning the Trade-Off between Gaining Energy and Avoiding Predation. Philosophical Transactions of the Royal Society of London B: Biological Sciences 341:375–397.

JOHNSON, C. J. AND M. P. GILLINGHAM. 2008. Sensitivity of species-distribution models to error, bias, and model design: An application to resource selection functions for woodland caribou. Ecological Modelling 213:143–155.

JOHNSON, C. J., D. R. SEIP AND M. S. BOYCE. 2004. A quantitative approach to conservation planning: using resource selection functions to map the distribution of mountain caribou at multiple spatial scales. Journal of Applied Ecology 41:238–251.

JOHNSON, D. H. 1980. The Comparison of Usage and Availability Measurements for Evaluating Resource Preference. Ecology 61:65–71.

JOHNSON, H. E., M. HEBBLEWHITE, T. R. STEPHENSON, D. W. GERMAN, B. M. PIERCE AND V. C. BLEICH. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

JOHNSON, H. E., L. S. MILLS, T. R. STEPHENSON AND J. D. WEHAUSEN. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

KAITALA, A., V. KAITALA AND P. LUNDBERG. 1993. A Theory of Partial Migration. American Naturalist 142:59–81.

KEATING, K. A., P. J. P. GOGAN, J. M. VORE AND L. R. IRBY. 2007. A Simple Solar Radiation Index for Wildlife Habitat Studies. The Journal of Wildlife Management 71:1344–1348.

KUDO, G. 1991. Effects of Snow-Free Period on the Phenology of Alpine Plants Inhabiting Snow Patches. Arctic and Alpine Research 23:436–443.

LACK, D. 1968. Bird Migration and Natural Selection. Oikos 19:1–&.

LELE, S. R., E. H. MERRILL, J. KEIM AND M. S. BOYCE. 2013. Selection, use, choice and occupancy: clarifying concepts in resource selection studies. Journal of Animal Ecology 82:1183–1191.

LIMA, S. AND L. DILL. 1990. Behavioral Decisions Made Under the Risk of Predation - a Review and Prospectus. Canadian Journal of Zoology-Revue Canadienne De Zoologie 68:619–640.

LIU, C., P. M. BERRY, T. P. DAWSON AND R. G. PEARSON. 2005. Selecting thresholds of occurrence in the prediction of species distributions. Ecography 28:385–393.

LUNDBERG, P. 1988. The evolution of partial migration in Birds. Trends in Ecology & Evolution 3:172–175.

MANLY, B. F., L. MCDONALD, D. THOMAS, T. L. MCDONALD AND W. P. ERICKSON. 2002. Resource Selection by Animals: Statistical Design and Analysis for Field Studies. Springer Netherlands.

MÅRELL, A., A. HOFGAARD AND K. DANELL. 2006. Nutrient dynamics of reindeer forage species along snowmelt gradients at different ecological scales. Basic and Applied Ecology 7:13–30.

MCDONALD, T. L. 2013. The point process use-availability or presence-only likelihood and comments on analysis. Journal of Animal Ecology 82:1174–1182.

MEYER, C. B. AND W. THUILLER. 2006. Accuracy of resource selection functions across spatial scales. Diversity and Distributions 12:288–297.

MILNER-GULLAND, E. J., J. M. FRYXELL AND A. R. E. SINCLAIR. 2011. Animal Migration: A Synthesis. OUP Oxford.

MONTGOMERY, D. C., E. A. PECK AND G. G. VINING. 2012. Introduction to Linear Regression Analysis. John Wiley & Sons.

MORALES, J. M. ET AL. 2010. Building the bridge between animal movement and population dynamics. Philosophical Transactions of the Royal Society B: Biological Sciences 365:2289–2301.

MYSTERUD, A., L.-B. LIAN AND D. Ø. HJERMANN. 1999. Scale-dependent trade-offs in foraging by European roe deer (Capreolus capreolus) during winter. Canadian Journal of Zoology 77:1486–1493.

MYSTERUD, A., L. E. LOE, B. ZIMMERMANN, R. BISCHOF, V. VEIBERG AND E. MEISINGSET. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos 120:1817–1825.

NELSON, M. E. 1995. Winter range arrival and departure of white-tailed deer in northeastern Minnesota. Canadian Journal of Zoology 73:1069–1076.

NICHOLSON, M. C., R. T. BOWYER AND J. G. KIE. 1997. Habitat selection and survival of mule deer: Tradeoffs associated with migration. Journal of Mammalogy 78:483–504.

PETTORELLI, N., J. O. VIK, A. MYSTERUD, J.-M. GAILLARD, C. J. TUCKER AND N. C. STENSETH. 2005. Using the satellite-derived NDVI to assess ecological responses to environmental change. Trends in Ecology & Evolution 20:503–510.

PULLIAM, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RETTIE, W. J. AND F. MESSIER. 2000. Hierarchical habitat selection by woodland caribou: its relationship to limiting factors. Ecography 23:466–478.

RITTGER, K., T. H. PAINTER AND J. DOZIER. 2013. Assessment of methods for mapping snow cover from MODIS. Advances in Water Resources 51:367–380.

ROBINSON, R. A. ET AL. 2009. Travelling through a warming world: climate change and migratory species. Endangered species research 7:87–99.

SAPPINGTON, J. M., K. M. LONGSHORE AND D. B. THOMPSON. 2007. Quantifying Landscape Ruggedness for Animal Habitat Analysis: A Case Study Using Bighorn Sheep in the Mojave Desert. The Journal of Wildlife Management 71:1419–1426.

SCHROEDER, C. A., R. T. BOWYER, V. C. BLEICH AND T. R. STEPHENSON. 2010. Sexual Segregation in Sierra Nevada Bighorn Sheep, Ovis canadensis sierrae: Ramifications for Conservation. Arctic, Antarctic, and Alpine Research 42:476–489.

SENFT, R., M. COUGHENOUR, D. BAILEY, L. RITTENHOUSE, O. SALA AND D. SWIFT. 1987. Large Herbivore Foraging and Ecological Hierarchies. Bioscience 37:789–&.

SOBERÓN, J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. Ecology Letters 10:1115–1123.

SPITZ, D. 2015. “migrateR”: tools for animal movement classification.

TELFER, E. AND J. KELSALL. 1984. Adaptation of Some Large North-American Mammals for Survival in Snow. Ecology 65:1828–1834.

U. S. FISH AND WILDLIFE SERVICE. 2007. Recovery plan for the Sierra Nevada bighorn sheep. U. S. Fish and Wildlife Service, Sacramento, California, USA.

WALKER, A. B. D., K. L. PARKER, M. P. GILLINGHAM, D. D. GUSTINE AND R. J. LAY. 2007. Habitat selection by female Stone's sheep in relation to vegetation, topography, and risk of predation. Ecoscience 14:55–70.

WHITE, K. S., N. L. BARTEN, S. CROUSE AND J. CROUSE. 2013. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

WILCOVE, D. S. AND M. WIKELSKI. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.

WORTON, B. J. 1989. Kernel Methods for Estimating the Utilization Distribution in Home-Range Studies. Ecology 70:164–168.

ZWEIFEL-SCHIELLY, B., M. KREUZER, K. C. EWALD AND W. SUTER. 2009. Habitat selection by an Alpine ungulate: the significance of forage characteristics varies with scale and season. Ecography 32:103–113.

TABLE 4-1. AIC scores for naive and behavioral models of first-order resource selection (i.e. population range selection) by Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). The naive model includes interactions allowing for seasonal differences in resource selection (i.e. winter v summer). Additionally, the behavioral model includes interactions accounting for strategy-specific differences in winter selection by migrants and residents.

	ΔAIC	**Parameters**	**AIC Wt.**
Behavioral	0	46	0
Naive	365	28	1

TABLE 4-2. Parameter estimates, standard errors and Wald statistics (z) for models of resource selection by Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* in the Sierra Nevada mountains of California. Top model results are shown for each combination of strategy/season (migrant, resident, summer, winter) and scale (S1, S2, S3). Blank values indicate non-significant terms.

A) First-order selection

	Migrant			Resident			Winter			Summer		
Parameter	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**
aspect												
elevation	-4.98	0.30	-16.69	-4.43	0.31	-14.10	-5.21	0.29	-17.82	-4.73	0.30	-15.71
elevation^2	6.57	0.28	23.22	6.57	0.28	23.20	6.99	0.28	25.12	6.57	0.28	23.22
escape distance	-1.17	0.08	-13.89	-1.34	0.10	-12.96	-1.19	0.06	-19.28	-0.88	0.08	-10.87
escape terrain	0.23	0.07	3.23	0.19	0.05	3.62	0.18	0.05	3.59	0.19	0.05	3.59
fractional snow cover	-1.60	0.08	-19.20	-2.09	0.11	-19.45	-1.63	0.07	-23.74	-1.35	0.08	-17.29
NDVI	25.53	1.54	16.61	54.96	2.28	24.10	34.38	1.25	27.49	18.14	1.38	13.14
NDVI^2	-29.88	1.74	-17.17	-64.22	2.65	-24.26	-40.11	1.42	-28.23	-21.66	1.57	-13.82
slope	0.33	0.16	2.11	0.79	0.19	4.23	0.32	0.04	7.78	0.28	0.14	1.99
slope^2				-0.68	0.18	-3.72						
snow free patch size	-0.52	0.05	-9.98	-0.52	0.05	-9.93	-0.50	0.05	-9.72	-0.52	0.05	-9.98
SRI	-0.42	0.05	-8.82	-0.23	0.04	-6.20	-0.33	0.04	-8.90	-0.23	0.04	-6.27
trees	-0.30	0.05	-6.24	-0.75	0.06	-12.48	-0.50	0.04	-13.51	-0.42	0.05	-9.19
VRM												
elev*slope	-0.58	0.11	-5.45	-0.89	0.08	-11.23	-0.82	0.06	-12.75	-0.89	0.08	-11.25
escd*NDVI				0.90	0.35	2.60	0.31	0.21	1.43	-1.31	0.24	-5.34
escd*trees	-1.06	0.10	-10.22	-1.06	0.10	-10.21	-1.22	0.08	-15.40	-1.37	0.12	-11.31
esct*NDVI	0.52	0.18	2.96				0.34	0.14	2.44			
FSnow*SRI	-1.07	0.06	-17.05	-1.07	0.06	-17.10	-1.09	0.06	-17.61	-1.07	0.06	-17.05
NDVI*esct												
NDVI*FSnow				-2.24	0.29	-7.83	-0.60	0.19	-3.24	0.28	0.21	1.34
NDVI*trees	-0.26	0.11	-2.36	-0.26	0.11	-2.37				-0.26	0.11	-2.36

B) Second-order selection

	Migrant			Resident			Winter			Summer		
Parameter	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**
aspect												
elevation	2.81	0.30	9.47	-5.88	0.44	-13.29	-0.26	0.04	-7.01	-2.54	0.23	-10.92
elevation^2	-3.27	0.28	-11.57	5.66	0.40	14.05				2.23	0.22	10.18
escape distance	-0.53	0.06	-8.53	-0.80	0.06	-12.48	-0.63	0.04	-14.13	-0.46	0.03	-13.87
escape terrain										-0.07	0.03	-2.31
fractional snow cover	-0.17	0.04	-3.98	0.08	0.06	1.50	-0.13	0.03	-4.08			
NDVI	3.17	0.63	5.03	5.20	0.95	5.47	4.42	0.54	8.26	0.85	0.43	1.98
NDVI^2	-3.68	0.65	-5.70	-5.29	0.97	-5.46	-4.75	0.55	-8.60	-1.03	0.44	-2.36
slope	0.72	0.12	5.92				0.23	0.04	5.93	0.20	0.04	5.47
slope^2	-0.36	0.11	-3.33									
snow free patch size	-0.21	0.04	-5.28	-0.44	0.06	-7.35	-0.29	0.03	-9.36	-0.18	0.03	-5.53
SRI	0.34	0.03	10.07	0.12	0.05	2.66	0.24	0.03	9.17	0.20	0.03	7.61
trees	-0.18	0.04	-5.01	-0.15	0.05	-3.21	-0.19	0.03	-6.71	-0.10	0.03	-3.56
VRM	0.06	0.02	2.53									
elev*slope				-0.39	0.08	-4.89	-0.23	0.05	-4.45	-0.57	0.04	-13.58
escd*NDVI	0.52	0.09	5.74				0.41	0.07	5.52			
escd*trees							-0.22	0.07	-3.22			
esct*NDVI												
FSnow*SRI	-0.26	0.06	-4.39	-0.68	0.08	-8.15	-0.41	0.05	-8.63	-0.38	0.05	-7.79
NDVI*esct	0.15	0.06	2.47				0.13	0.05	2.50			
NDVI*FSnow										-0.22	0.07	-3.34
NDVI*trees	0.50	0.08	6.19				0.36	0.07	5.45			

C) Third-order selection

	Migrant			**Resident**			**Winter**			**Summer**		
Parameter	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**	**Estimate**	**SE**	**z**
aspect	-0.09	0.04	-1.96									
elevation	1.14	0.11	10.69	5.25	0.47	11.21	4.86	0.33	14.53	2.40	0.31	7.85
elevation^2				-3.29	0.43	-7.73	-3.10	0.31	-9.91	-1.23	0.28	-4.39
escape distance	-1.72	0.24	-7.15	-1.89	0.10	-19.37	-1.70	0.09	-18.36	-1.26	0.07	-18.31
escape terrain	0.09	0.08	1.12	-0.14	0.05	-2.88	-0.05	0.04	-1.33	-0.05	0.04	-1.38
fractional snow cover	-1.31	0.09	-14.96	-1.97	0.05	-39.30	-1.83	0.04	-43.70	-1.22	0.04	-32.23
NDVI	11.64	1.61	7.24	26.84	1.33	20.12	23.42	1.04	22.62	20.51	0.84	24.55
NDVI^2	-11.89	1.64	-7.26	-27.74	1.39	-19.94	-24.22	1.08	-22.50	-21.43	0.87	-24.66
slope	3.23	0.43	7.58				1.43	0.16	8.95	2.26	0.14	15.99
slope^2	-2.79	0.34	-8.23				-1.27	0.13	-9.70	-1.82	0.12	-15.23
snow free patch size	0.52	0.06	8.12	-0.45	0.06	-7.81						
SRI	1.01	0.08	13.28	-0.05	0.04	-1.10	0.17	0.04	4.64	0.49	0.03	15.05
trees	-0.73	0.14	-5.18	-0.78	0.10	-7.92	-0.83	0.09	-9.78	-0.68	0.06	-10.99
VRM	0.08	0.04	2.03	0.23	0.02	9.62	0.19	0.02	9.71	0.08	0.02	3.88
elev*slope	-2.33	0.17	-14.08	-1.17	0.09	-13.50	-1.50	0.08	-19.87	-1.48	0.07	-20.46
escd*NDVI										-0.49	0.18	-2.72
escd*trees	-1.75	0.49	-3.54	-1.11	0.34	-3.21	-1.33	0.28	-4.73	-1.33	0.21	-6.26
esct*NDVI				-0.25	0.08	-3.10	-0.36	0.07	-5.53			
FSnow*SRI				-0.31	0.08	-3.96	-0.30	0.06	-4.76	-0.14	0.06	-2.44
NDVI*esct	-0.66	0.12	-5.45							-0.46	0.07	-6.31
NDVI*FSnow	-0.62	0.17	-3.73	-2.09	0.14	-14.88	-1.70	0.10	-17.68	-1.71	0.08	-20.31
NDVI*trees							0.29	0.09	3.17			

TABLE 4-3. Spearman Rank Correlations correlating Sierra Bighorn resource selection functions and observed probability of use using internal re-substituted training data for validation. Values in italics indicate results for models being tested at the scale for which they were developed. Values in bold are predictions from scale-integrated models. Associated p-values <0.001 for all correlation coefficients shown.

		Behavioral			**Naive**		
	Model	**Study Area**	**Population Range**	**Individual Range**	**Study Area**	**Population Range**	**Individual Range**
Migrant	First-order RSF	*1*	0.985	0.72	*0.988*	0.997	0.975
	Second-order RSF	0.988	*1*	1	1	*1*	0.963
	Third-order RSF	1	0.997	*0.969*	1	1	*0.966*
	SRSF	**0.988**	**0.988**	**0.899**	**0.988**	**0.988**	**0.928**
Resident	First-order RSF	*1*	1	0.969	*1*	0.997	0.969
	Second-order RSF	1	*1*	0.969	1	*1*	0.988
	Third-order RSF	0.997	0.997	*0.937*	1	0.997	*0.937*
	SRSF	**0.988**	**0.988**	**0.937**	**0.988**	**0.997**	**0.937**

TABLE 4-4. Spearman Rank Correlations correlating Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* resource selection functions and observed probability of use using external withheld testing data for validation. Values in italics indicate results for models being tested at the scale for which they were developed. Values in bold are predictions from scale-integrated models. Associated p-values <0.001 for all correlation coefficients shown.

		Behavioral		**Naive**	
	Model	**Population Range**	**Individual Range**	**Population Range**	**Individual Range**
Migrant	First-order RSF	0.96	0.889	1	0.985
	Second-order RSF	*1*	1	*1*	0.997
	Third-order RSF	1	*0.969*	1	*0.969*
	SRSF	**0.997**	**0.966**	**0.988**	**0.988**
Resident	First-order RSF	0.988	0.966	0.988	0.966
	Second-order RSF	*0.988*	0.969	*1*	0.969
	Third-order RSF	0.969	*0.937*	0.988	*0.969*
	SRSF	**0.988**	**0.937**	**0.988**	**0.969**

TABLE 4-5. Comparison of the fit between summer and migrant (winter) predictions for locations used by resident Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* in winter using k-folds cross validation. Values are spearman rank correlations showing the correlation between migrant and summer Sierra bighorn resource selection functions and the observed probability of use for resident locations. Associated p-values <0.001 for all correlation coefficients shown.

		Scale		
Prediction	**Study Area**	**Population Range**	**Individual Range**	**Integrated**
Migrant	1	0.976	0.969	0.969
Summer	1	0.988	0.937	0.937

TABLE 4-6. Comparison of resident and migrant Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* use during winter at first (within population range) second (within population range) and third (within individual range) order scales.

	Migrant Mean	**Resident Mean**	**Difference/Obs. Range**	**P-Value**
First Order				
elevation	3004	3195	0.067	$< 1*10^{-5}$
distance to escape terrain	93.2	89.78	-0.002	0.14
slope	29.36	28.65	-0.01	$1*10^{-4}$
aspect	0.502	0.5	-0.002	0.51
VRM	0.009	0.008	-0.005	$< 1*10^{-5}$
SRI	0.669	0.696	0.023	$< 1*10^{-5}$
NDVI	102.1	99.9	-0.027	$< 1*10^{-5}$
fractional snow cover	0.663	0.707	0.044	$< 1*10^{-5}$
snow-free patch size	2.782	2.191	-0.012	$< 1*10^{-5}$
Second Order				
elevation	3001	3190	0.066	$< 1*10^{-5}$
distance to escape terrain	71.23	81.1	0.008	$< 1*10^{-5}$
slope	31.07	28.9	-0.032	$< 1*10^{-5}$
aspect	0.499	0.497	-0.002	0.71
VRM	0.01	0.008	-0.008	$< 1*10^{-5}$
SRI	0.681	0.674	-0.005	0.13
NDVI	101.8	99.53	-0.033	$< 1*10^{-5}$
fractional snow cover	0.642	0.706	0.065	$< 1*10^{-5}$
snow-free patch size	2.8	2.141	-0.013	$< 1*10^{-5}$
Third Order				
elevation	2874	3291	0.153	$< 1*10^{-5}$
distance to escape terrain	15.11	32.43	0.024	$< 1*10^{-5}$
slope	36.73	32.79	-0.059	$< 1*10^{-5}$
aspect	0.486	0.495	0.009	0.097
VRM	0.013	0.014	0.004	0.024
SRI	0.829	0.743	-0.082	$< 1*10^{-5}$
NDVI	103.5	99.7	-0.078	$< 1*10^{-5}$
fractional snow cover	0.458	0.584	0.128	$< 1*10^{-5}$
snow-free patch size	10.32	2.83	-0.153	$< 1*10^{-5}$

TABLE 4-7. AICc scores for models predicting the population-level prevalence of migratory behavior across 8 population of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) as a function of RSF predictions of suitable habitat. Model terms include the proportion of a population range predicted to be suitable exclusively for migrants (“migrant”), exclusively for residents (“resident”), suitable to both migrants and residents (“shared”), suitable for migrants (“migrant total” = “migrant” + “shared”) and suitable for residents (“resident total” = “resident” + “shared”).

	K	ΔAICc	AICcWt	Cum.Wt
Integrated Models				
migrant	3	0.00	0.76	0.76
migrant total	3	4.72	0.07	0.83
resident total	3	4.81	0.07	0.90
resident	3	4.86	0.07	0.97
migrant + shared	4	6.74	0.03	0.99
migrant total + resident total	4	11.03	0.00	1.00
resident + shared	4	11.31	0.00	1.00
resident + migrant + shared	5	19.16	0.00	1.00
S1 Models				
migrant	3	0.00	0.86	0.86
migrant total	3	5.31	0.06	0.92
resident total	3	5.70	0.05	0.97
migrant + shared	4	7.86	0.02	0.98
migrant total + resident total	4	7.86	0.02	1.00
S2 Models				
migrant total	3	0.00	0.60	0.60
resident total	3	2.70	0.16	0.76
migrant	3	2.95	0.14	0.90
resident	3	3.86	0.09	0.98
migrant total + resident total	4	9.05	0.01	0.99
migrant + shared	4	9.20	0.01	1.00
resident + shared	4	10.15	0.00	1.00
resident + migrant + shared	5	27.19	0.00	1.00
S3 Models				
migrant total	3	0.00	0.33	0.33
migrant	3	0.34	0.27	0.60
resident total	3	1.00	0.20	0.80
resident	3	1.04	0.19	0.99
migrant total + resident total	4	9.10	0.00	0.99
migrant + shared	4	9.18	0.00	1.00
resident + shared	4	9.74	0.00	1.00
resident + migrant + shared	5	27.74	0.00	1.00

FIGURE 4-1. Example schematic of hierarchically nested sampling design for modeling habitat selection across three scales for migrant and resident Sierra Nevada bighorn sheep in California's Sierra Nevada Mountains. Example shows data for two individuals (one migrant, one resident) from the Mount Langley sub-population.

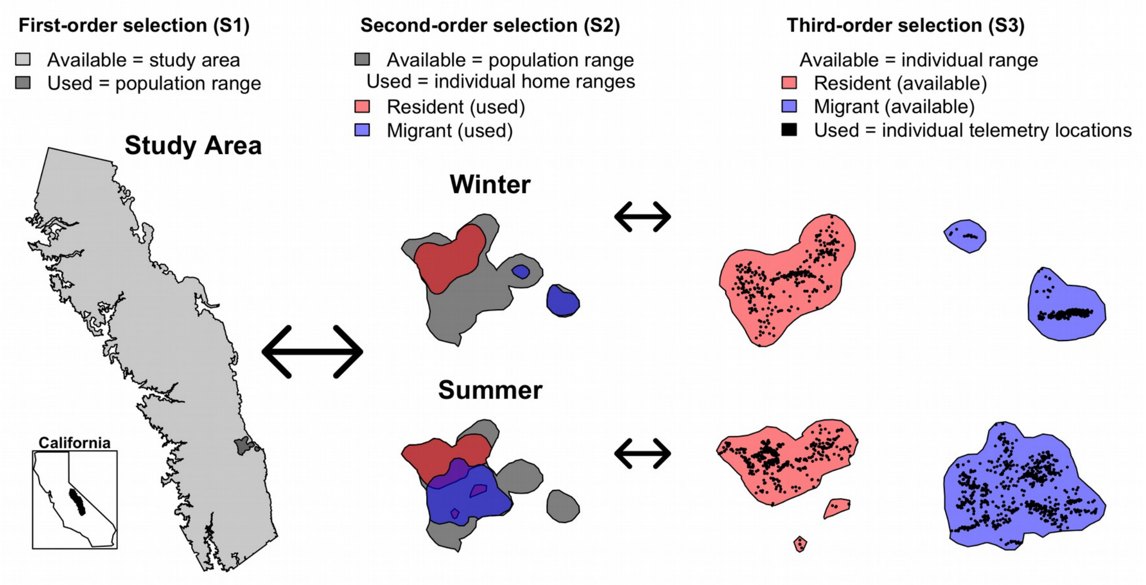


FIGURE 4-2. Spatial example of predictions for locations suitable to residents (red),migrants (blue) and both (purple). Areas in white represent locations within the population range that are suitable for neither migrants nor residents. Axes shown give coordinates in Universal Transverse Mercator (UTM).

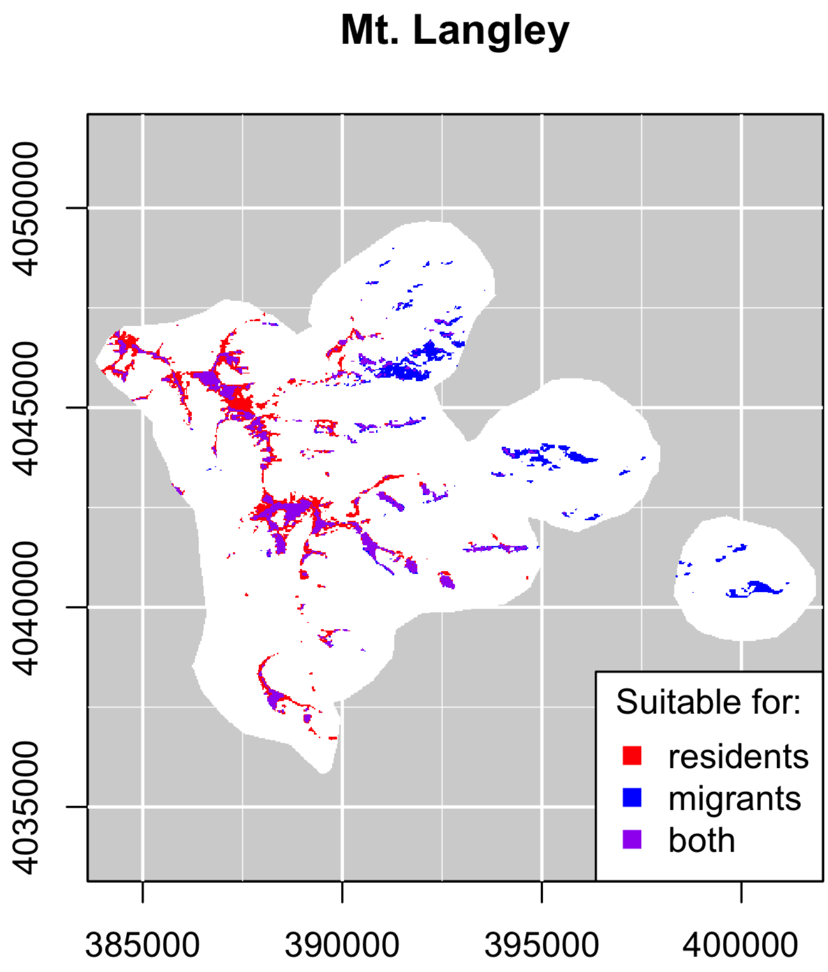
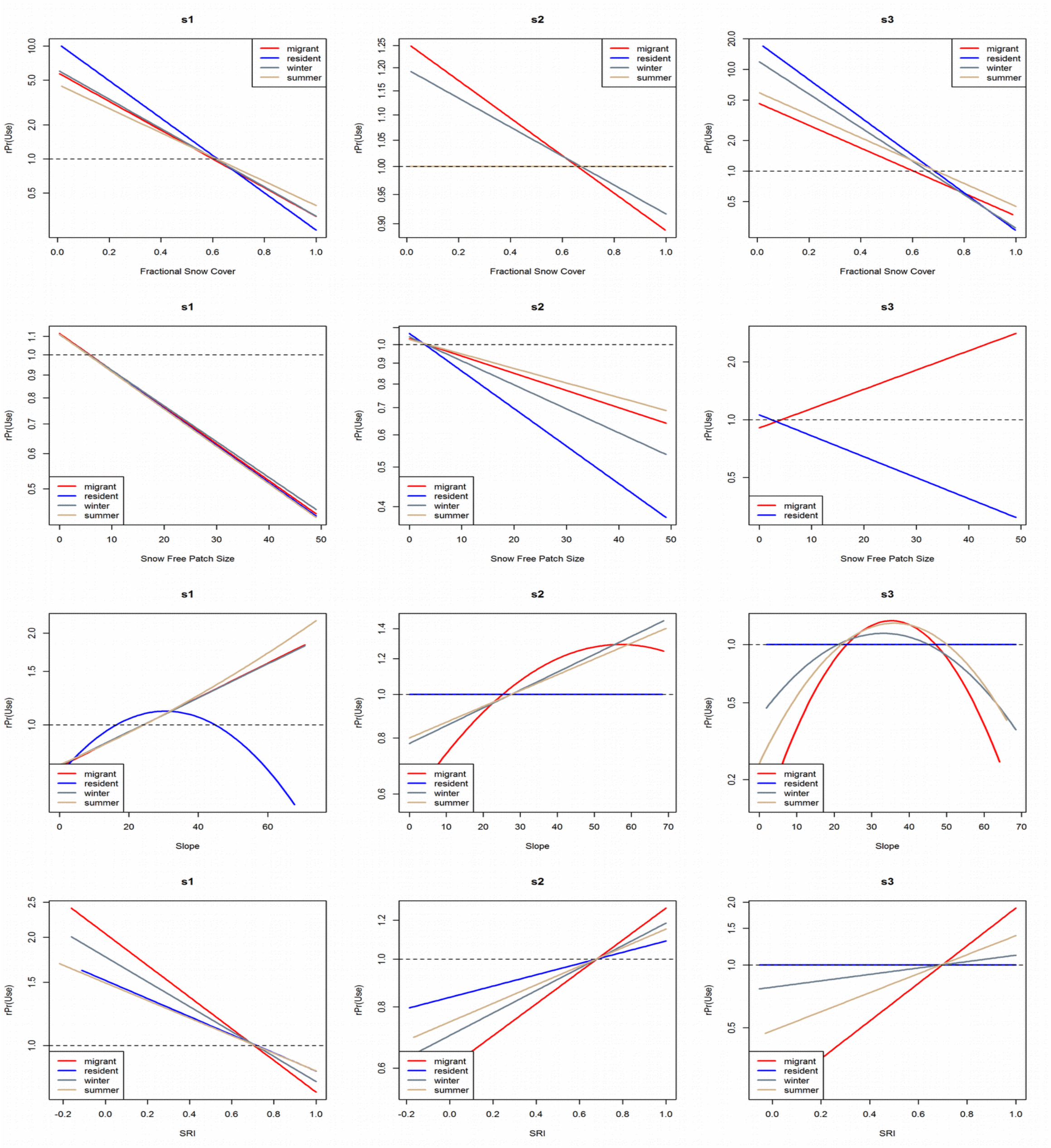


FIGURE 4-3. Examples of contrasting selection between migrants and residents that are masked when migratory behavior is ignored. Left to right plots show first through third-order differences in predicted selection between migrant, resident and naive (winter) models for four covariates, top to bottom: fractional snow cover, snow-free patch size, solar radiation index (SRI) and slope. Non-significant terms were omitted. Included are three terms whose 95% confidence intervals overlapped zero (shown as horizontal lines; second order: resident snow free patch size, third order: resident snow-free patch size and slope).


s1
s2
s3
rPr(Use)
Fractional Snow Cover
0.0 0.2 0.4 0.6 0.8 1.0
0.5 1.0 2.0 5.0 10.0
0.90 0.95 1.00 1.05 1.10 1.15 1.20 1.25
0.5 1.0 2.0 5.0 10.0 20.0
migrant
resident
winter
summer
Snow Free Patch Size
0 10 20 30 40 50
0.5 0.6 0.7 0.8 0.9 1.0 1.1
0.4 0.5 0.6 0.7 0.8 0.9 1.0
0.5 1.0 2.0
Slope
0 20 40 60
1.0 1.5 2.0
0 10 20 30 40 50 60 70
0.6 0.8 1.0 1.2 1.4
0.2 0.5 1.0
SRI
-0.2 0.0 0.2 0.4 0.6 0.8 1.0
1.0 1.5 2.0 2.5
0.6 0.8 1.0 1.2
0.5 1.0 1.5 2.0

CHAPTER 5.

WHAT MAKES THEM MOVE? TESTING PROXIMATE CAUSES AND CONSEQUENCES OF MIGRATION[4]

Migratory behavior has been noted for its ecological importance, ubiquity across taxa and world-wide decline (Wilcove and Wikelski 2008; Bauer and Hoye 2014). Migration is chiefly understood as a strategy for taking advantage of resources that vary cyclically and is often associated with strongly seasonal environments (Dingle and Drake 2007). Migratory status is rarely fixed at the population level, instead some proportion of most migratory populations display resident behavior, a phenomenon known as partial migration (Chapman et al. 2011). Partial migrants face variable environments in which they must rely on cues to make behavioral decisions that will affect their fitness in an uncertain future. The demographic success of partial migrants can depend on their ability to appropriately match their migratory status (migrant vs. resident, Gillis et al. 2008; Alves et al. 2013) and tactics (e.g. timing and duration of movement) to the conditions they experience (Post and Forchhammer 2008; Gienapp and Bregnballe 2012). The way partial migrants rely on cues to determine their migratory behavior thus has major demographic implications that are central to the conservation of migration (Berger 2004; Bolger et al. 2008; Wilcove and Wikelski 2008).

Any theory of partial migration is challenged with explaining how migrant and resident strategies have been able to coexist through evolutionary time (Lundberg 1987).

---

[4] This paper is formatted for submission to Movement Ecology with Mark Hebblewhite and Tom Stephenson as coauthors.

Although migratory behavior is often assumed to be fixed at the individual level, research on many taxa supports the hypothesis that migratory stratus is plastic at the individual level and depends on phenotype (Adriaensen and Dhondt 1990; Brodersen et al. 2008; Grayson et al. 2011; Skov et al. 2011; Chapter 3). This emerging evidence supporting the conditional basis of partial migration warrants revisiting questions about the extent of commonalities in migratory behavior across taxa (Dingle 2006). Research shows similarities among birds (Adriaensen and Dhondt 1990), fish (Skov et al. 2011) and amphibians (Grayson et al. 2011), where partial migration is maintained by each status carrying condition-dependent risks and rewards; for individuals in the best physical condition, residency is less risky than migration, but the reverse is true for animals in poorer physical condition. Importantly, this condition-dependence in migratory behavior is also consistently observed to create disparities in the demographic performance of migrants and residents (Adriaensen and Dhondt 1990; Grayson et al. 2011; Skov et al. 2011). In European robins (*Erithracus rubecula*), for example, poor condition individuals lack the energetic stores required to survive northern winters and thus undertake migration as an alternative to certain death (Adriaensen and Dhondt 1990). These individuals who migrate, however, suffer lower survival and reproductive success compared to those that remain resident, leading several authors to describe migration as a making the "best of a bad job" (Lundberg 1987; Adriaensen and Dhondt 1990; Gillis et al. 2008; Chapman et al. 2011; Grayson et al. 2011; Skov et al. 2011). Still, for most taxa the basis of an individual's migratory status remains contentious and poorly understood.

Among ungulates, studies of the determinants of migratory status remain scarce despite the ecological and economic importance of migration in this taxonomic group (Gordon et al. 2004; Bolger et al. 2008; Bauer and Hoye 2014). Morrison and Bolger (2012) showed that migratory status in wildebeest is determined in part by an individual's reproductive history. Recent work by (Eggeman et al. 2016) showed that migratory propensity in a herd of partially migratory elk *Cervus elaphus* was codetermined by external (winter severity, predator abundance) and internal (age) cues. These examples of the importance of internal cues fill a key gap, explaining how differences in migratory status can arise within a single population that experiences the same set of external conditions. Without this conditionality, partial migration can only be explained through recourse to long-term equivalence in demographic performance between migrants and residents through evolutionary time (Lundberg 1988).

Research on migration has largely focused on determining how external cues influence migratory tactics (e.g. Meunier et al. 2008). In facing environmental uncertainly an individual's condition (i.e. age, nutritional condition, reproductive status) may determine the relative riskiness of specific behaviors and therefore may play a significant role in determining how an animal migrates (Monteith et al. 2011). In temperate systems, for example, snow deposited in early-season storms can punish delayed migration to winter range by increasing movement costs. Monteith et al. (2011) showed that increasing nutritional condition and age both delay the timing of fall migration in mule deer *Odocoileus hemionus.* The authors interpreted these results as suggesting that good physical condition buffers individuals from the potential consequences of delayed migration, effectively making the behavior less risky for fatter animals, but that older animals also engage in riskier behavior because, compared to younger animals, they have fewer remaining reproductive opportunities left to lose (Monteith et al. 2011). Despite the research emphasis placed on external cues, a better understanding of internal cues may prove crucial in attempting to quantify plasticity in migratory behavior, its population consequences, and thus, its conservation (Bolger et al. 2008).

One consequence of partial migration is that the conditions individuals experience vary as a function of their migratory behavior (Chapter 4). These differences can determine the relative success of migrant and resident strategies and thus carry major demographic implications. The conditions individuals experience combine with individual characteristics (e.g. age; Ezard et al. 2007) to determine vital rates and ultimately the rate of population growth. In birds, fish, amphibians and invertebrates, numerous studies indicate that migration represents a losing strategy in which individuals are forced to "make the best of a bad situation" (e.g. Gillis et al. 2008; Grayson et al. 2011; Skov et al. 2011). While data on migration in mammals remain more limited, an example from the ungulate literature shows that fitness trade-offs can instead lead migrants and residents to have equivalent demographic success (Hebblewhite and Merrill 2011). Like other long-lived species, we expect ungulate population growth to be driven by recruitment with adult survival remaining high and constant (Gaillard et al. 1998) as a result of evolutionary canalization (Gaillard and Yoccoz 2003). Consequently, migratory-status-specific demographic differences are most likely to manifest in rates of pregnancy and in the survival of younger age-classes (Post and Forchhammer 2008; Gaillard 2013) both of which depend on the ability of adult females to pay the high energetic cost of gestation and lactation. Access to improved nutrition is one of the main hypothesized benefits of migratory behavior in mammals (Fryxell et al. 1988; Hebblewhite et al. 2008). Therefore we might expect status-specific differences in reproductive success to arise from the difference in conditions experienced by migrants and residents, but these differences may also be a major cause of migratory behavior. Adult ungulates that avoid the expense of lactation enter winter with larger energy reserves and in some harsh environments a strategy of reproduction in alternating years even enhances individual fitness (Cook et al. 2004; Testa 2004). Thus if reproductive success varies with migratory status, we might also expect the difference in energetic expense between successful and failed reproductive efforts to influence an individuals choice of migratory strategy in the following year. Morrison and Bolger (2012) observed reproductive success to influence an individual's migratory status in the following year, suggesting that wildebeest fluctuate between migratory and resident status in a pattern of alternating reproduction. Still, there have been few direct tests of demographic differences between migrants and residents, especially among ungulates. Understanding if (and how) migrants and residents differ in their demographic contribution has important implications for the persistence of migratory behavior and the distribution and persistence of migratory species in the face of climate change (Bolger et al. 2008; Robinson et al. 2009; Festa-Bianchet 2013).

North America's rarest ungulate, federally-endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae,* hereafter Sierra bighorn) are partially migratory alpine specialist found only in a single mountain range in California (U. S. Fish and Wildlife

Service 2007). Migration in Sierra bighorn is a conditional strategy, with individuals frequently switching between years (Chapter 3). In summer, Sierra bighorn share large high-elevation ranges, but in winter some individuals migrate to lower elevation ranges, while others remain year-round high-elevation residents. Lambing in this species occurs mid-April to mid-March, concurrent or immediately following return movement of migrants to shared high-elevation range (Chapter 3). Thus migrants and residents experience different conditions during gestation and early lactation. Migrants access higher quality forage on their low-elevation winter ranges and are expected to face lower-energetic demands for thermoregulation and locomotion compared to migrants (Telfer and Kelsall 1984; Goodson et al. 1991; Chapter 4). These energetic advantages are, however, purchased at the cost of greater predation risk, setting up a classic risk-forage trade-off (Festa-Bianchet 1988). Low-elevation ranges lead to greater overlap with predator species including Sierra bighorn's main predator cougars (*Puma concolor;* Johnson et al. 2012). Like many temperate herbivores, Sierra sheep are most nutritionally stressed in late spring and early summer when their energetic expenditure peaks with late gestation and lactation (Clutton-Brock 1984).

We hypothesize that internal cues will be more important for predicting an individual’s migratory status (migration v. residency) and that external cues will have greater explanatory power relative migratory tactics (timing and duration of movement), vindicating the emphasis placed on external cues in past research. We focus here on determining the proximate causes of plasticity in three specific components of migratory behavior in Sierra bighorn: 1) determinants of migratory status (migrant, resident); 2) timing of migration; and 3) duration of migration. For each component of migratory behavior (status, timing, duration) we test whether behavior depends on internal cues, external cues or a combination of both. Lastly, we examine two fitness corollary, adult survival and summer lambing status, to test for migratory-status-specific differences in the demographic success of migrants and residents. We hypothesize that migrants and residents in this system display demographic balancing through a forage-predation trade off in which migrants purchase higher reproductive success at the cost of lower adult survival.

Methods

Study System

Sierra Nevada bighorn sheep (Sierra bighorn hereafter) are only found in the southern half of the Sierra Nevada Mountains California, USA. With a mean height of around 3000m, the southern half of this range is characterized by a steep escarpment along its eastern face that connects the bulk of the range's alpine habitat to sagebrush steppe over 2,500m below (Hill 1975). In winter precipitation at higher elevations falls as snow, while the rain shadow the range creates keeps its eastern slopes xeric year round. Sierra bighorn share large summer ranges at high elevation where they take advantage of nutrition from moist subalpine meadows (U. S. Fish and Wildlife Service 2007). In fall some individuals migrate to lower elevation for the duration of winter, while others remain year-round residents on their high-elevation ranges (Chapter 2). Furthermore, we know that migratory behavior in Sierra bighorn is plastic; individuals not only alter their tactics, but also frequently change their migratory status between years (Chapter 3).

Data Collection

We captured Sierra bighorn ewes using a helicopter and net-gun in fall (late October) and winter (March-April) 2006 – 2012 (University of Montana IACUC AUP 046-11, Federal Fish and Wildlife Service Permit No. TE050122-4). During winter captures we used an ultrasound to check adults for pregnancy. Before release, we weighed and outfitted each female with very high frequency collars. We also affixed ear tags, which, in combination with the collars, allowed for the visual identification of unique individuals in the field. During late spring and early summer we used radio-telemetry to locate collared females from the ground. We then used spotting scopes to extensively observed these individuals for nursing behavior to determine if a lamb was at heel (Festa-Bianchet 1988; Portier et al. 1998; Rioux-Paquette et al. 2011). Sierra bighorn typically lamb in a narrow window from late spring to early summer, with most births occurring in May and June, but births can occur as early as mid-April or as late as Early July (Wehausen 1996; Portier et al. 1998). Hence lambing in Sierra bighorn immediately follows the return movement of migrants in spring (beginning in March; Chapter 3). These observations thus encompass information on both pregnancy and neonatal survival. Multiple attempts were made to confirm the lambing status of each marked female (May-August). For known-pregnant ewes, we estimate the probability of sighting/resighting (given known lamb status *sensu* Bonenfant et al. 2005) a lamb as 0.86 (SE = 0.064, n=29 known pregnant ewes). This rate is lower than that values previously recorded for moose

(*Alces alces* 0.97; Testa 2004) and elk(0.93; Hebblewhite and Merrill 2011), but higher than red deer (0.81; Bonenfant et al. 2005). With an average of 2.29 observations per ewe per year, we have on average only a 1% chance of missing a lamb. We do not expect the temporal differences in our observation of lambing status to be confounded by juvenile survival, because our observations follow neonatal mortality and nearly all remaining juvenile mortality occurs over winter (Portier et al. 1998). Finally, while low rates of twinning have been observed in other bighorn subspecies, we are not aware of any instances of twining in Sierra bighorn.

Quantifying Migration

We quantified migratory behavior in Sierra bighorn using non-linear modeling methods adapted from Bunnefeld et al. (2011) presented in Chapters 2 and 3. Elevation data was extracted for each of an individual's locations and these data were used to fit a set of a priori models each representing a different movement behavior. Individual migratory status was then determined by comparing this a priori model set using AIC (Burnham and Anderson 2002) to determine which behavior was best supported. One of the benefits of quantifying migration in this way is that migrant models include parameters describing the timing and duration of migratory movements, such that each classification of migratory behavior is accompanied by parameters that describe the individuals' tactics (i.e. the timing and duration of movement). See chapters 2 and 3 for further details.

Modeling Migratory Behavior

We tested plasticity in three separate components of migratory behavior. First, we used logistic regression (Hosmer et al. 2013) to model an individual's probability of migrating in each year. Second, we modeled the factors influencing the initiation of migratory movement using Cox proportional hazard models (Cox 1972). Third, we used Poisson regression to model the factors explaining the duration of migratory movements (Zuur et al. 2009). For timing and duration, we used separate models for fall and spring behavior. Our modeling approach was consistent across all models. First we separately fit “internal” and “external” models, sequentially removing non-significant terms to find a best model (*sensu* Hosmer et al. 2013). We then combined the remaining internal and external terms in a single combined model, which also included potential interactions between these terms, when biologically relevant. Internal cues included weight (kg), whether the female was observed with a lamb during the preceding spring, whether the female was still lactating in fall (i.e. as determined during animal capture), percent body fat as estimated based on ultrasound (Stephenson et al. 2002) and age. We also included a quadratic term for age to allow for non-linear relationships (e.g. similarities between young and senescing individuals). External cues included the mean elevation of the summer range (as estimated by non-linear classification models), the elevational distance migrated, an index of winter severity and an index of conditions during the preceding growing season. We used the elevation distance migrated only in models of migratory tactics, since the status-specific nature of this precluded its use in models of migratory status. For our index of large-scale climate conditions, we relied on the Southern

Oscillation Index (SOI), which has been shown to correlate with climatic conditions and ungulate migratory phenology in the Western US (Trenberth and Hurrell 1994; Stenseth et al. 2003). Consistent with these trends, previous work in the Sierra Nevada by Monteith et al. (2011) found a negative relationship between SOI and snowfall and weaker evidence of a positive relationship between SOI and mean annual temperature. Thus years with low SOI values tend to have higher snowfall and colder temperatures, representing more severe winters. We used seasonal averages of standardized SOI (National Oceanic and Atmospheric Administration, Climate Prediction Center) an index of winter severity and growing season conditions (December-March and May-September, respectively).

Our classification models provided direct estimates of the duration of migratory movement (estimated as the time required to complete ½ to ¾ movement), which we use for our models of duration. Our movement models, however, only provide estimates of the midpoint of migratory movements. For our models of migratory timing, we therefore estimated the onset of migratory movement as the midpoint minus two times the duration from ½ to ¾ completion. All analyses were performed in program R (R Core Team 2014) with the help of the migrateR package (Chapter 2).

Consequences of Migration

We modeled survival of GPS-collared adult females using Cox proportional hazard models (Hosmer et al. 2011). To test for differences in risk associated with migrant and resident ranges, we fit a series of a priori models including terms for age, elevation, and the population mean summer elevation. Testing for differences in elevation, rather than migratory status, allowed us to increase our sample size by including data from incomplete animal-years, which we were unable to confidently classify as migrant or resident (e.g. animal-years ending in early winter mortality). We compared these models and determined a top model using AICc (Burnham and Anderson 2002). All models were stratified by population because hazards (probability of survival) crossed between populations (Hosmer et al. 2011).

We modeled the factors affecting our spring observation of lamb-at-heel (1, no lamb, 0) using logistic regression (Hosmer et al. 2013). To test our hypotheses we fit and compared 3 *a priori* models: first, a model including only a term for winter severity, but no term for migratory status; second a combined model including the effects of both status and winter severity; and third an interaction model in which the effect of migratory status on spring lambing depends on winter severity. To quantify winter severity, we averaged standardized SOI values (National Oceanic and Atmospheric Administration, Climate Prediction Center) across the winter months (December-March) preceding the lambing season. All models also included lambing status in the preceding year, age and a quadratic of age to allow for reduced reproductive activity in young and senescent individuals. We thus only analyzed animal-years in which individual's spring lambing status was determined, where the individuals spring lambing status from the preceding year was known and the individual was two or more years old (i.e. was capable of having lambed in the preceding year). We identified a top model using AICc, evaluated support for this model using AICc weights and evaluating the importance of the included terms based on their parameter estimates and associated p-values. We did not account for repeat measures as they represented only a small fraction of our total data.

Results

We captured and radiocollared 113 adult female Sierra bighorn from 2006 – 2012 from 8 populations, collecting 214 animal-years of spatial data. We monitoring 145 animal-years from 4 populations for survival estimation. We were able to assess the survival consequences of migration and reproduction using 75 animal-years of data with known migratory and reproductive status. Finally, of these 75 ewes, we quantified movement behavior and identified annual lambing status for 48 animal-years of data including 12 instances of residency and 36 of migration, for which fall measurements of body mass and lactation status were also available. Winter severity significantly explained migratory propensity ($p = 0.039$) and our top model also included an interaction between body weight and fall-lactation status ($p = 0.081$; Table 5-1; Figure 5-1). Propensity to migrate increased with increasing winter severity and for females who had been observed lactating in the preceding fall, but this difference was only observed among individuals of average to below-average weight (Table 5-1). As body weight increased, migratory propensity increased among non-lactating females, but decreased among lactating females (Figure 5-1). The migratory propensity of non-lactating females of average or below-average weight remained difficult to predict.

In fall, lactating females and females that had been observed with lambs in the spring migrated earlier (Table 5-1). In spring animals migrated earlier in response to fair weather and when larger altitudinal distance separated winter and summer ranges (Table 5-1). Similar to fall timing, the duration of fall movements also depended on whether a female was observed to have a lamb-at-heel, but was also influenced by the elevation of the summer range (Table 5-1). Individuals with higher summer ranges migrated more quickly in fall, but having a lamb-at-heel decreased the speed at which individuals migrated (Table 5-1). Finally, the duration of spring movements depended weakly on age ($p < 0.10$) with young and old individuals moving more quickly (Table 5-1).

We used n=146 animal-years from 4 populations that included 15 mortalities to test for the consequences of migratory behavior to adult female survival. Across populations, survival decreased with age (p-vaule = 0.002), but we observed no effect of elevation or mean elevation in summer (Table 5-2). To test the reproductive consequences of migration, we analyzed all animal years for which our data on internal cues were complete (n = 75) animal-years including 54 cases of migration and 21 cases of residency representing data from 52 unique individuals. On average, 63% of Sierra bighorn were observed with lambs in spring/summer. Contrary to our hypothesis that migration carried reproductive benefits, ewes were more likely to have lambs following residency than migration with 76% of residents (95% CI: 0.58 – 0.94) observed with lambs, compared to only 57 % of migrants (95% CI: 0.48 – 0.67). Our combined model received the greatest support (AICc weight = 0.54), with our interactive and winter-only models receiving similar support (AICc weights = 0.25 and 0.21, respectively; Table 5-1). Migratory status was the best-supported term in our top model ($p < 0.06$). The estimate for this term was negative, confirming that compared to migrants, residents were more likely to be observed with a lamb in spring. All models provided marginal support for the inclusion of both age terms ($p < 0.10$) and in all cases the linear term was positive and the quadratic term negative, indicating that spring lambing observations were consistently high across most age classes, but started lower for the youngest age classes and dropped off steeply for older individuals (age >10) suggesting senescence. No models provided support for the importance of SOI or lambing status in the previous year. The interaction between SOI and migratory status was also unsupported, confirming that weather effects acted similarly on both strategies.

Discussion

Internal and external cues both play an integral role in determining migratory status and tactics. Contrary to our first hypothesis that internal cues should predominate determination of migratory status, we found that an external cue played the most important role in determining whether or not an animal migrated, but that migratory status was also influenced by an interaction between two internal cues. This dependence of migratory status on internal and external cues provides a possible explanation of partial migration in this system that is consistent with theory (Lundberg 1988; Kaitala et al. 1993) and capable of explaining both the presence of migration and residency within the same population and variation in migratory propensity through time. Contrary to the research emphasis placed on external cues, we also found internal cues to be important to the timing of fall movement and the duration of migration in both seasons. Thus our results also contradicted our second hypothesis, that migratory tactics would chiefly be determined by external cues. Only spring migration was unambiguously dominated by external cues supporting the hypothesized importance of spring phenology in driving migratory behavior (Fryxell et al. 1988; Albon and Langvatn 1992; Hebblewhite et al. 2008). While we should still expect external cues to provide insight into the mechanisms driving migratory behavior, understanding if, when and why individuals respond differently to these cues is a key aspect of partial migration that is still missing from our understanding of this behavior in most systems.

Our results emphasize the similarities in the pattern of partial migration across diverse taxonomic groups. The dependence of migratory propensity on body mass that we observe is consistent with the broader dependence of migratory behavior on conditional risk that has previously been observed in a variety of non-mammalian vertebrates (Adriaensen and Dhondt 1990; Gillis et al. 2008; Grayson et al. 2011; Skov et al. 2011). Winter storms put resident Sierra bighorn at risk of starvation by unpredictably increasing energetic demands and limiting access to forage. This risk is heightened for femalees that enter winter nutritionally stressed following the demands of calf-rearing and summer lactation (Cook et al. 2004; Middleton et al. 2013). The demands of summer lactation may thus force all but the fattest ewes with young-at-heel to migrate to recoup the energetic reserves they expended during the preceding year (Figure 5-1). Individuals with lower energetic expenditure, including non-reproductive ewes and ewes who lost lambs early, may thus have greater flexibility in trading forage for reduced predation risk. These results are consistent with recent work emphasizing the importance of summer nutrition in ungulates (Cook et al. 2004; Monteith et al. 2011; Middleton et al. 2013), but are also novel insomuch as we are amongst the first studies to demonstrate that migratory behavior may also be affected by nutritional costs of reproduction.

However, our results differ in a number of ways from previous studies of migration in other ungulate systems. We failed to find an effect of age on migratory status, which Eggeman et al. (2016) observed influenced the probability of status switching in elk, with older migrants being less likely and older residents more likely to change migratory status compared to their younger counterparts. Similarly, we failed to observe an effect of age on the timing of migration, although this has been observed in other ungulates. Monteith et al. (2011) showed that, like animals in good nutritional condition, older female mule deer and those in better nutritional condition migrated later in fall. Both Monteith et al. (2011) and Eggeman et al. (2016) interpreting these results as supporting the hypothesis that like individuals in good condition, older individuals are less risk averse—while good condition individuals were buffered from the negative consequences associated with early-season storms that punish delayed migration to winter range, older individuals were more willing to accept risks because compared to younger individuals they have fewer remaining reproductive opportunities at stake (Clutton-Brock 1984). Lendrum et al. (2013) also observed a condition dependent change in mule deer migratory timing, with animals in better condition migrating earlier in the spring when late season storms made movement more risky. In some systems, age may correlate with other internal cues, such that some cues (e.g. changes in body condition) become more likely with age. Thus the influence of age is difficult to prove because the significance of this term can depend on the available amount and quality of data on other internal cues.

We also observed the presence of young to decrease the duration of migratory movement, the opposite relationship that Singh and Ericsson (2014) observed in moose. This difference may be explained by a discrepancy in the cost of migration for these species. Moose, like other long-distance migrants, experience elevated predation risk while migrating, presumably a combined effect of predator density and the navigation of novel environments (Hebblewhite and Merrill 2011; White et al. 2013). Where migratory movements are themselves risky, increasing the speed of movement may improve juvenile survival by decreasing the time over which risk accrues. Sierra bighorn, on the other hand, migrate relatively short distances along an altitudinal gradient, are expected to experienced the greatest predation risk on their low-elevation winter range and are unlikely to encounter predators while moving between ranges (Johnson et al. 2012). Hence the earlier and longer migratory movements of Sierra bighorn would not necessarily expose juveniles to any additional risk. Instead, slower movements may benefit migrants by allowing them to exploit resources en route. Previous work on bighorn sheep shows that lactating ewes spend more time foraging in the fall compared to non-lactating ewes (Ruckstuhl and Festa-Bianchet 1998). Whereas non-lactating females can afford to temporarily forgo foraging to make quick direct movements, the nutritional stress of lactation may drive ewes with lambs to feed continuously thus limiting their speed of travel.

Our results largely concur with previous work examining the effect of external cues on migratory plasticity. In contrast to the study of internal cues, literature surrounding external cues is well developed with broad agreement among studies. The broad-scale climate variable we used, SOI, encompasses temperature and other fine-scale weather measures which other studies have tested directly. For example, the broad taxonomic importance of temperature as a cue of migratory behavior is further supported by a wide array of evidence including recent studies explaining advances in the timing of bird migration in urban areas (Tryjanowski et al. 2013), as well as the ability of broad scale climate metrics to predict migration in aquatic species (Sims et al. 2001). Among ungulates, Monteith et al (2011) found fall migration by mule deer to respond to cooling weather and precipitation, especially accumulating snow. Studying white-tailed deer *Odocoileus virginianus*, Fieberg et al. (2008) found the proportion of migrants to depend on winter severity, but lacked the data required to test for the influence of internal cues as we do here. Similar to our results with Sierra bighorn, winter severity and topography were also found to influence the timing of fall migration in European roe deer (Cagnacci et al. 2011). Lastly, while our sample size is smaller than that in other studies (e.g. 335 animal-years, Fieberg et al. 2008; 297 animal-years Monteith et al. 2011; 603 animal-years, Eggeman et al. 2012), migration in bighorn also appears to be more variable than migration in other ungulate taxa (Chapter 2). For example, Sierra bighorn appear extremely flexible in migratory status boasting one of the highest rates of status switching so far recorded for any ungulate (Chapter 3). That, even in the face of this variation, our results are statistically significant emphasizes the potential importance of the cues we analyzed.

The reproductive consequences of migration that we detected carry serious implications for the conservation of Sierra bighorn, suggesting that in partially migratory populations high-elevation year-round residents have a greater per-capita contribution to population growth than do migrants. Although we failed to find the expected decrease in adult survival associated with migration (to lower elevation; Johnson et al. 2012), we can not rule out this relationship. Many of the mortalities we observed occurred to early in winter to confidently classify the individual's migratory status. Furthermore, differences in adult female survival can be difficult to detect due to low variation and even small differences in these rates can have large implications for ungulate demography (Gaillard et al. 1998). Reduced migrant survival is common among other systems in which migratory propensity depends on an individuals size or body condition (Gillis et al. 2008; Grayson et al. 2011; Skov et al. 2011). It is still possible that in spite of this demographic handicap Sierra bighorn achieve demographic balancing through a status-specific difference in overwinter juvenile survival. If the greater access to forage migrants enjoy (Chapter 4) allows migrants to make larger maternal investments, this might increasing the overwinter survival of their offspring compared to residents due to carryover effects (Portier et al. 1998). This effect would have to be large to counterbalance the difference in lambing we observed. Demographic balancing has been observed in other ungulate systems (Hebblewhite and Merrill 2011). Overwinter juvenile survival remains a crucial gap in our knowledge of Sierra sheep demography. As with many questions surrounding migration, our ability to test these questions depends on the collection of long-term data needed to estimate the reproductive success of specific individuals (Gaillard 2013).

Other authors have interpreted the reduced demographic success of migrants as representing a losing strategy (e.g., Adriaensen and Dhondt 1990; Skov et al. 2011). Our results, however contradict this suggestion. In three of the sub-populations of Sierra bighorn we studied, we have yet to observe any resident behavior (Chapter 3). Previous research has nonetheless shown that these all-migrant sub-populations are capable of supporting a high abundance of Sierra bighorn, even serving as source populations that have seeded neighboring recolonizations (Johnson et al. 2010; Chapter 3; California Department of Fish and Game, unpublished data). Hence migration is not a losing strategy, but a conditional strategy whose success depends on context. Migration allows Sierra bighorn to persist in areas that are too resource poor to support year around residency. Migration thus complements residency in extending the species distribution (Fryxell et al. 1988). Migrant-only populations may be especially important in maintaining demographic and genetic connectivity in a metapopulation context (Pulliam 2000; Johnson et al. 2010). The lower demographic success of migrants, however, suggests that these populations are likely to be more vulnerable to anthropogenic stressors. Based on the greater per-capita demographic contributions of residents, we recommend that reintroduction efforts for this species focus on the identification and protection of high-elevation ranges capable of supporting residency.

In our analysis of Sierra bighorn we were unable to account for density, an external cue which is likely an important driver of migratory behavior. Previous studies have shown lifetime reproductive success to be inversely related to density and escape from negative density-dependent effects has been hypothesized as one of the major benefits of migration (McLoughlin et al. 2006; Mysterud et al. 2011). Changes in the timing of migration associated with density have been interpreted as evidence that density plays a conditional role in determining migratory behavior (Plumb et al. 2009; Mysterud et al. 2011). Further evidence for migrants showing conditional response to density is offered by Plumb et al.'s (2009) observation of the frequency of migration increasing with population size from a small, reintroduced population in which initially no migratory behavior was observed. More recently, Eggeman et al. (2016) showed that status-switching between years was density dependent in a partially-migratory elk herd and that migration in this system was increasingly favored as elk abundance increased. We would thus expect the effect of density on migratory status to be similar to that of SOI, with higher densities increasing migratory propensity for all animals, but disproportionally affecting individuals that are smaller or in poor condition.

Literature Cited

Adriaensen, F. and A. A. Dhondt. 1990. Population-Dynamics and Partial Migration of the European Robin (Erithacus rubecula) in Different Habitats. Journal of Animal Ecology 59:1077–1090.

Albon, S. and R. Langvatn. 1992. Plant Phenology and the Benefits of Migration in a Temperate Ungulate. Oikos 65:502–513.

Alves, J. A. et al. 2013. Costs, benefits, and fitness consequences of different migratory strategies. Ecology 94:11–17.

Bauer, S. and B. J. Hoye. 2014. Migratory animals couple biodiversity and ecosystem functioning worldwide. Science (New York, N.Y.) 344:1242552.

Berger, J. 2004. The last mile: How to sustain long-distance migration in mammals. Conservation Biology 18:320–321.

Bolger, D. T., W. D. Newmark, T. A. Morrison and D. F. Doak. 2008. The need for integrative approaches to understand and conserve migratory ungulates. Ecology Letters 11:63–77.

Bonenfant, C., J.-M. Gaillard, F. Klein and J.-L. Hamann. 2005. Can we use the young : female ratio to infer ungulate population dynamics? An empirical test using red deer Cervus elaphus as a model. Journal of Applied Ecology 42:361–370.

Brodersen, J., P. A. Nilsson, L.-A. Hansson, C. Skov and C. Brönmark. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. Ecology 89:1195–1200.

Bunnefeld, N. et al. 2011. A model-driven approach to quantify migration patterns: individual, regional and yearly differences. Journal of Animal Ecology 80:466–476.

Burnham, K. P. and D. R. Anderson. 2002. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

Cagnacci, F. et al. 2011. Partial migration in roe deer: migratory and resident tactics are end points of a behavioural gradient determined by ecological factors. Oikos 120:1790–1802.

Chapman, B. B., C. Brönmark, J.-Å. Nilsson and L.-A. Hansson. 2011. The ecology and evolution of partial migration. Oikos 120:1764–1775.

CLUTTON-BROCK, T. H. 1984. Reproductive Effort and Terminal Investment in Iteroparous Animals. American Naturalist 123:212–229.

COOK, J. G. ET AL. 2004. Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. Wildlife Monographs:1–61.

COX, D. 1972. Regression Models and Life-Tables. Journal of the Royal Statistical Society Series B-Statistical Methodology 34:187–+.

DINGLE, H. 2006. Animal migration: is there a common migratory syndrome? Journal of Ornithology 147:212–220.

DINGLE, H. AND V. A. DRAKE. 2007. What Is Migration? BioScience 57:113–121.

EGGEMAN, S., M. HEBBLEWHITE AND E. H. MERRILL. 2016. Behavioral flexibility in migratory behavior in a long-lived ungulate. Journal of Animal Ecology In Press.

EZARD, T. H. G., P. H. BECKER AND T. COULSON. 2007. Correlations between age, phenotype, and individual contribution to population growth in common terns. Ecology 88:2496–2504.

FAIRHURST, E. N., D. J. GREEN, R. H. MACKAS, H. A. MIDDLETON, C. A. MORRISSEY AND I. B. J. WHITEHORNE. 2010. Altitudinal migration in American Dippers (Cinclus mexicanus): do migrants produce higher quality offspring? Canadian Journal of Zoology 88:369.

FESTA-BIANCHET, M. 1988. Seasonal range selection in bighorn sheep: conflicts between forage quality, forage quantity, and predator avoidance. Oecologia 75:580–586.

FESTA-BIANCHET, M. 2013. Human-induced reversal of fortunes for migratory ungulates? Ecology 94:1243–1244.

FIEBERG, J., D. W. KUEHN AND G. D. DELGIUDICE. 2008. Understanding variation in autumn migration of northern white-tailed deer by long-term study. Journal of Mammalogy 89:1529–1539.

FRYXELL, J., J. GREEVER AND A. SINCLAIR. 1988. Why Are Migratory Ungulates so Abundant. American Naturalist 131:781–798.

GAILLARD, J.-M. 2013. Assessing fitness consequences of migratory tactics requires long-term individually based monitoring. Ecology 94:1261–1264.

GAILLARD, J.-M., M. FESTA-BIANCHET AND N. G. YOCCOZ. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

GAILLARD, J. M. AND N. G. YOCCOZ. 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology 84:3294–3306.

GIENAPP, P. AND T. BREGNBALLE. 2012. Fitness Consequences of Timing of Migration and Breeding in Cormorants. PLoS ONE 7:e46165.

GILLIS, E. A., D. J. GREEN, H. A. MIDDLETON AND C. A. MORRISSEY. 2008. Life history correlates of alternative migratory strategies in american dippers. Ecology 89:1687–1695.

GOODSON, N., D. STEVENS AND J. BAILEY. 1991. Effects of Snow on Foraging Ecology and Nutrition of Bighorn Sheep. Journal of Wildlife Management 55:214–222.

GORDON, I. J., A. J. HESTER AND M. FESTA-BIANCHET. 2004. REVIEW: The management of wild large herbivores to meet economic, conservation and environmental objectives. Journal of Applied Ecology 41:1021–1031.

GRAYSON, K. L., L. L. BAILEY AND H. M. WILBUR. 2011. Life history benefits of residency in a partially migrating pond-breeding amphibian. Ecology 92:1236–1246.

HEBBLEWHITE, M. AND E. H. MERRILL. 2011. Demographic balancing of migrant and resident elk in a partially migratory population through forage–predation tradeoffs. Oikos 120:1860–1870.

HEBBLEWHITE, M., E. MERRILL AND G. MCDERMID. 2008. A multi-scale test of the forage maturation hypothesis in a partially migratory ungulate population. Ecological Monographs 78:141–166.

HILL, M. 1975. Geology of the Sierra Nevada. University of California Press.

HOSMER, D. W. J., S. LEMESHOW AND R. X. STURDIVANT. 2013. Applied Logistic Regression. John Wiley & Sons.

HOSMER, D. W. J., S. LEMESHOW AND M. SUSAN. 2011. Applied Survival Analysis: Regression Modeling of Time to Event Data. John Wiley & Sons.

JOHNSON, H. E., M. HEBBLEWHITE, T. R. STEPHENSON, D. W. GERMAN, B. M. PIERCE AND V. C. BLEICH. 2012. Evaluating apparent competition in limiting the recovery of an endangered ungulate. Oecologia 171:295–307.

JOHNSON, H. E., L. S. MILLS, T. R. STEPHENSON AND J. D. WEHAUSEN. 2010. Population-specific vital rate contributions influence management of an endangered ungulate. Ecological Applications 20:1753–1765.

KAITALA, A., V. KAITALA AND P. LUNDBERG. 1993. A Theory of Partial Migration.

American Naturalist 142:59–81.

LENDRUM, P. E., C. R. ANDERSON JR, K. L. MONTEITH, J. A. JENKS AND R. T. BOWYER. 2013. Migrating Mule Deer: Effects of Anthropogenically Altered Landscapes. PLoS ONE 8:e64548.

LUNDBERG, P. 1987. Partial bird migration and evolutionarily stable strategies. Journal of Theoretical Biology 125:351–360.

LUNDBERG, P. 1988. The evolution of partial migration in Birds. Trends in Ecology & Evolution 3:172–175.

MCLOUGHLIN, P. D., M. S. BOYCE, T. COULSON AND T. CLUTTON-BROCK. 2006. Lifetime reproductive success and density-dependent, multi-variable resource selection. Proceedings of the Royal Society of London B: Biological Sciences 273:1449–1454.

MEUNIER, J. ET AL. 2008. Proximate Cues for a Short-Distance Migratory Species: an Application of Survival Analysis. The Journal of Wildlife Management 72:440–448.

MIDDLETON, A. D. ET AL. 2013. Animal migration amid shifting patterns of phenology and predation: lessons from a Yellowstone elk herd. Ecology 94:1245–1256.

MONTEITH, K. L. ET AL. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. Ecosphere 2:art47.

MORRISON, T. A. AND D. T. BOLGER. 2012. Wet season range fidelity in a tropical migratory ungulate. Journal of Animal Ecology 81:543–552.

MYSTERUD, A., L. E. LOE, B. ZIMMERMANN, R. BISCHOF, V. VEIBERG AND E. MEISINGSET. 2011. Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos 120:1817–1825.

PLUMB, G. E., P. J. WHITE, M. B. COUGHENOUR AND R. L. WALLEN. 2009. Carrying capacity, migration, and dispersal in Yellowstone bison. Biological Conservation 142:2377–2387.

PORTIER, C., M. FESTA-BIANCHET, J.-M. GAILLARD, J. T. JORGENSON AND N. G. YOCCOZ. 1998. Effects of density and weather on survival of bighorn sheep lambs (Ovis canadensis). Journal of Zoology 245:271–278.

POST, E. AND M. C. FORCHHAMMER. 2008. Climate change reduces reproductive success of an Arctic herbivore through trophic mismatch. Philosophical Transactions of the Royal Society of London B: Biological Sciences 363:2367–2373.

PULLIAM, H. R. 2000. On the relationship between niche and distribution. Ecology Letters 3:349–361.

R CORE TEAM. 2014. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

RIOUX-PAQUETTE, E., M. FESTA-BIANCHET AND D. W. COLTMAN. 2011. Sex-differential effects of inbreeding on overwinter survival, birth date and mass of bighorn lambs. Journal of Evolutionary Biology 24:121–131.

ROBINSON, R. A. ET AL. 2009. Travelling through a warming world: climate change and migratory species. Endangered species research 7:87–99.

RUCKSTUHL, K. E. AND M. FESTA-BIANCHET. 1998. Do Reproductive Status and Lamb Gender Affect the Foraging Behavior of Bighorn Ewes? Ethology 104:941–954.

SIMS, D. W., M. J. GENNER, A. J. SOUTHWARD AND S. J. HAWKINS. 2001. Timing of squid migration reflects North Atlantic climate variability. Proceedings of the Royal Society of London B: Biological Sciences 268:2607–2611.

SINGH, N. J. AND G. ERICSSON. 2014. Changing motivations during migration: linking movement speed to reproductive status in a migratory large mammal. Biology Letters 10:20140379.

SKOV, C. ET AL. 2011. Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society of London B: Biological Sciences 278:1414–1418.

STENSETH, N. C. ET AL. 2003. Review article. Studying climate effects on ecology through the use of climate indices: the North Atlantic Oscillation, El Niño Southern Oscillation and beyond. Proceedings of the Royal Society of London B: Biological Sciences 270:2087–2096.

STEPHENSON, T. R., V. C. BLEICH, B. M. PIERCE AND G. P. MULCAHY. 2002. Validation of mule deer body composition using in vivo and post-mortem indices of nutritional condition. Wildlife Society Bulletin 30:557–564.

TELFER, E. AND J. KELSALL. 1984. Adaptation of Some Large North-American Mammals for Survival in Snow. Ecology 65:1828–1834.

TESTA, J. W. 2004. Population dynamics and life history trade-offs of moose (alces alces) in south-central alaska. Ecology 85:1439–1452.

TRENBERTH, K. E. AND J. W. HURRELL. 1994. Decadal atmosphere-ocean variations in the Pacific. Climate Dynamics 9:303–319.

TRYJANOWSKI, P., T. H. SPARKS, S. KUŹNIAK, P. CZECHOWSKI AND L. JERZAK. 2013. Bird Migration Advances More Strongly in Urban Environments. PLoS ONE 8:e63482.

U. S. FISH AND WILDLIFE SERVICE. 2007. Recovery plan for the Sierra Nevada bighorn sheep. U. S. Fish and Wildlife Service, Sacramento, California, USA.

WEHAUSEN, J. D. 1996. Effects of mountain lion predation on bighorn sheep in the Sierra Nevada and Granite Mountains of California. Wildlife Society Bulletin 24:471–479.

WHITE, K. S., N. L. BARTEN, S. CROUSE AND J. CROUSE. 2013. Benefits of migration in relation to nutritional condition and predation risk in a partially migratory moose population. Ecology 95:225–237.

WILCOVE, D. S. AND M. WIKELSKI. 2008. Going, going, gone: Is animal migration disappearing? PLoS Biology 6:e188.

ZUUR, A., E. N. IENO, N. WALKER, A. A. SAVELIEV AND G. M. SMITH. 2009. Mixed Effects Models and Extensions in Ecology with R. Springer Science & Business Media.

TABEL 5-1**.** Comparison of model results and parameter estimates from the top model explaining Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* migratory propensity, 2005-2014, Sierra Nevada mountain range, California, USA. The combined model included an effect for migratory status and winter severity, the interaction model included an interaction between these terms and the null model included an effect of winter severity but not migratory status. All models included effects for age, the quadratic of age and whether the female had been observed with a lamb in the preceding spring. The combined model received the greatest support. Estimates from this model support the importance of migratory status and provide slightly weaker support for the importance of age. The other terms were not supported.

Model	**K**	**AICc**	**ΔAICc**	**AICcWt**	**Cum.Wt**
Combined	6	102.4	0	0.54	0.54
Interaction	7	104.0	1.57	0.25	0.79
NULL	5	104.3	1.94	0.21	1

	Estimate	**Std. Error**	**z**	**Pr(>|z|)**
(Intercept)	0.08	1.29	0.06	0.95
migrant	-1.29	0.66	-1.96	0.05
age	0.85	0.47	1.82	0.07
age2	-0.07	0.04	-1.87	0.06
previous lamb	-0.81	0.56	-1.45	0.15
winter severity	-0.51	0.34	-1.49	0.14

TABLE 5-2 Top models of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* determination of migratory status and the duration and timing of movements in fall and spring 2005-2014, Sierra Nevada mountains, California USA. Choice of status and the duration of fall movements are codetermined by internal (e.g. weight, lamb) and external (e.g. southern oscillation index – SOI, summer elevation) cues. The duration of spring movements showed only a weak influence of a single internal cue, age. The more variable timing of fall migration was best explained by internal cues only (lactation and lambing). In contrast, the timing of spring migration, which is highly synchronous, was best predicted by external cues (altitudinal distance and SOI).

Model	**Term**	**Est.**	**Std. Error**	**t**	**Pr(>|t|)**
Status	Winter Severity	-12.808	6.209	-2.063	0.039
	Lactating	2.897	2.302	1.258	0.208
	Weight	5.033	3.253	1.547	0.122
	Lactating*Weight	-6.241	3.576	-1.745	0.081
Fall Duration	Summer Elevation	-0.004	0.002	-2.482	0.018
	Lamb	1.348	0.478	2.823	0.008
Spring Timing	Age	0.187	0.118	1.587	0.122
	Age^2	-0.018	0.01	-1.767	0.086

Model	**Term**	**Est.**	**Std. Error**	**z**	**Pr(>|z|)**	**exp(Est)**
Fall Timing	Lactating	0.871	0.454	1.919	0.055	2.388
	Lamb	1.461	0.5	2.921	0.003	4.309
Spring Timing	Altitudinal Distance	-0.003	0.001	-4.382	0	0.997
	Spring Severity	-0.973	0.375	-2.591	0.01	0.378

TABLE 5-3. Comparison of model results for adult female survival for Sierra Nevada bighorn sheep (*Ovis canadensis sierrae),* stratified by population. Risk increased with age, but was not influenced by elevation or the mean elevation of summer range.

Models	**K**	**ΔAICc**	**AICcWt**	**Cum.Wt**
Age	1	0	0.36	0.36
Age + Elev	2	0.52	0.28	0.64
Age + Mean(Elev)	2	0.87	0.23	0.87
Age + Elev + Mean(Elev)	3	2.25	0.12	0.98
Elev	1	7.01	0.01	0.99
Elev + Mean(Elev)	2	8.48	0.01	1

	Coef	**exp(Coef)**	**SE(Coef)**	**z**	**Pr(>|z|)**
Age	0.24	1.271	0.084	3.048	0.002

FIGURE 5-1. Example predictions of migratory propensity among Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). Predictions shown are for the Mt. Baxter population and are representative of the relationships observed among the six populations we examined. The propensity to migrate increased with increasing winter severity (top panel). Here winter severity is represented by the Southern Oscillation Index with values scaled such that 0 and 1 represent the mildest and most severe winter observed, respectively. Among lactating females, migratory propensity decreased with body weight (bottom panel). In contrast, among non-lactating females migratory propensity increased with body weight. The probability of migration among non-lactating females of average or below-average weight remains difficult to predict.

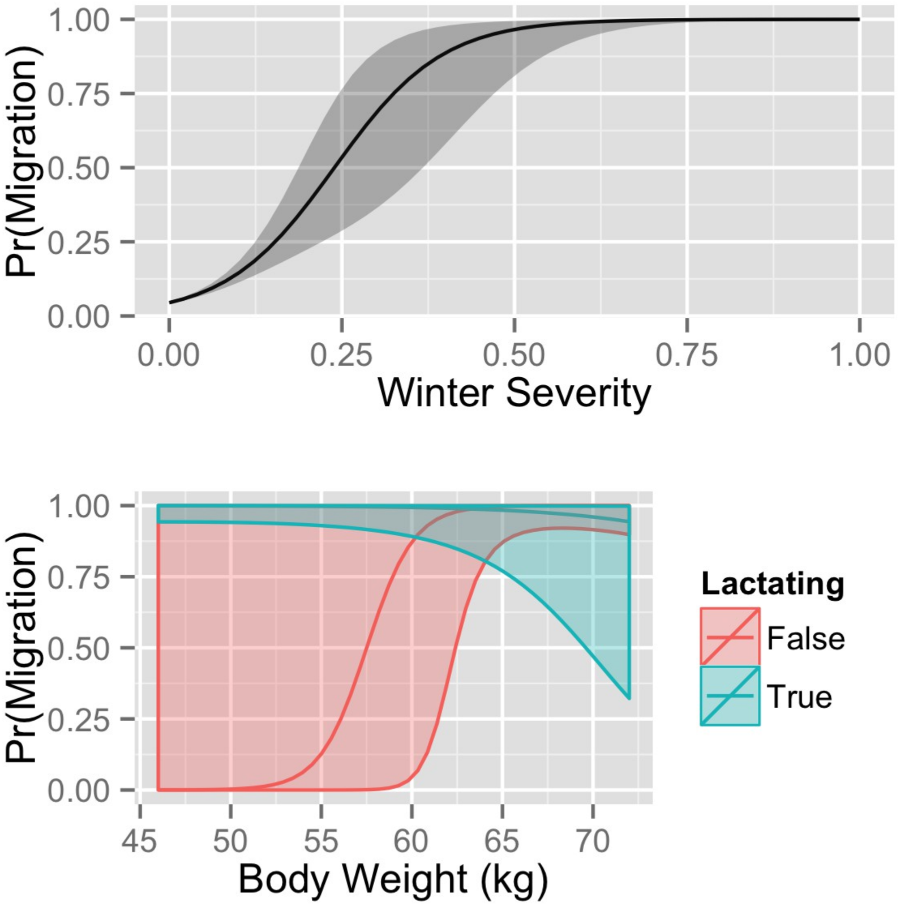


FIGURE 5-2. Cumulative migration curves with 95% confidence intervals illustrating the timing of spring and fall migration in Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) in the Sierra Nevada mountains, California, USA 2005-2014. Fall migration was more variable, beginning as early as October and ranging over five months. Spring migration was more synchronous, beginning as early as February, but with over 90% of animals moving in only two months: March and April.

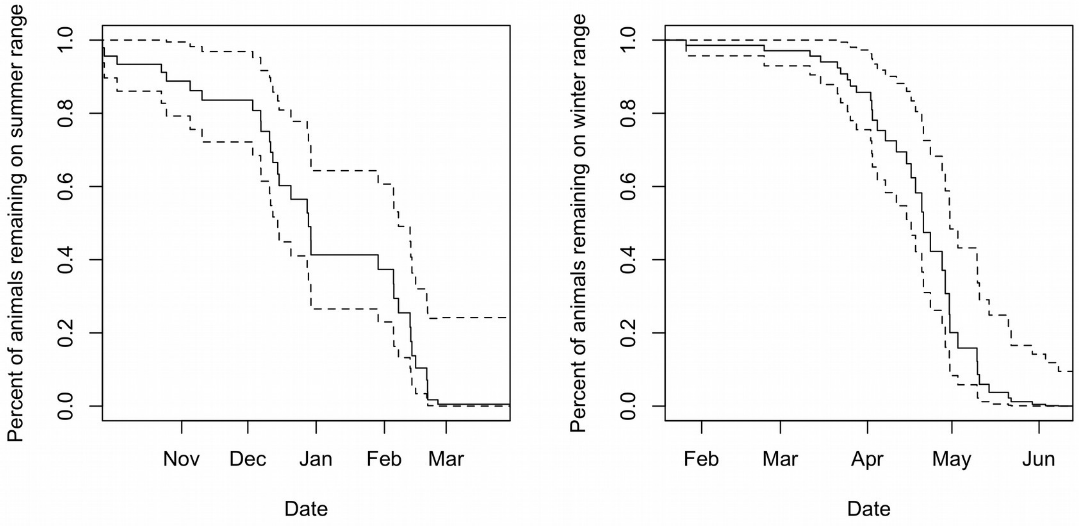
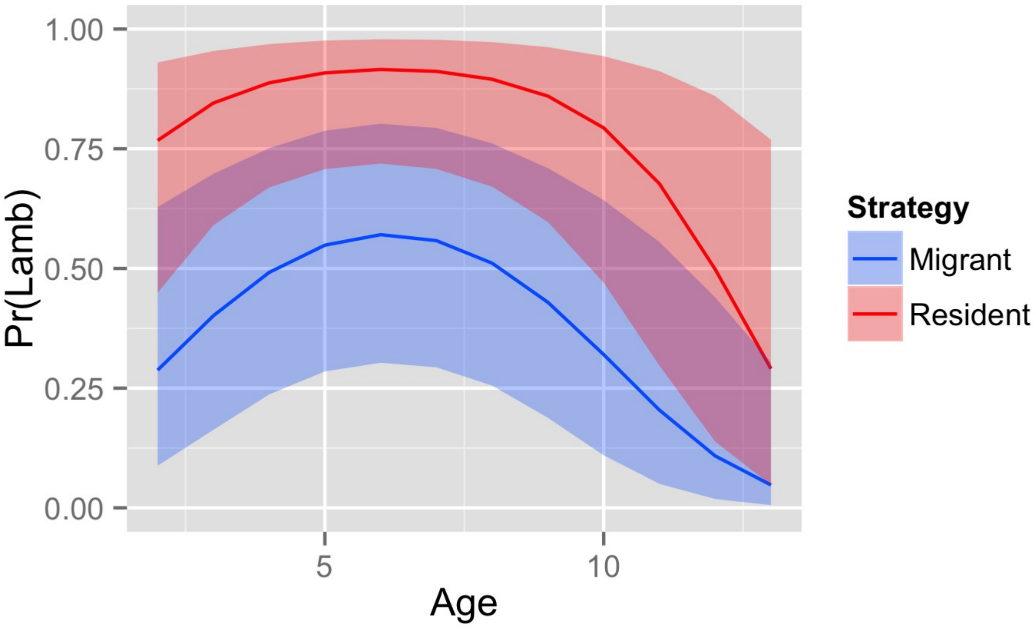
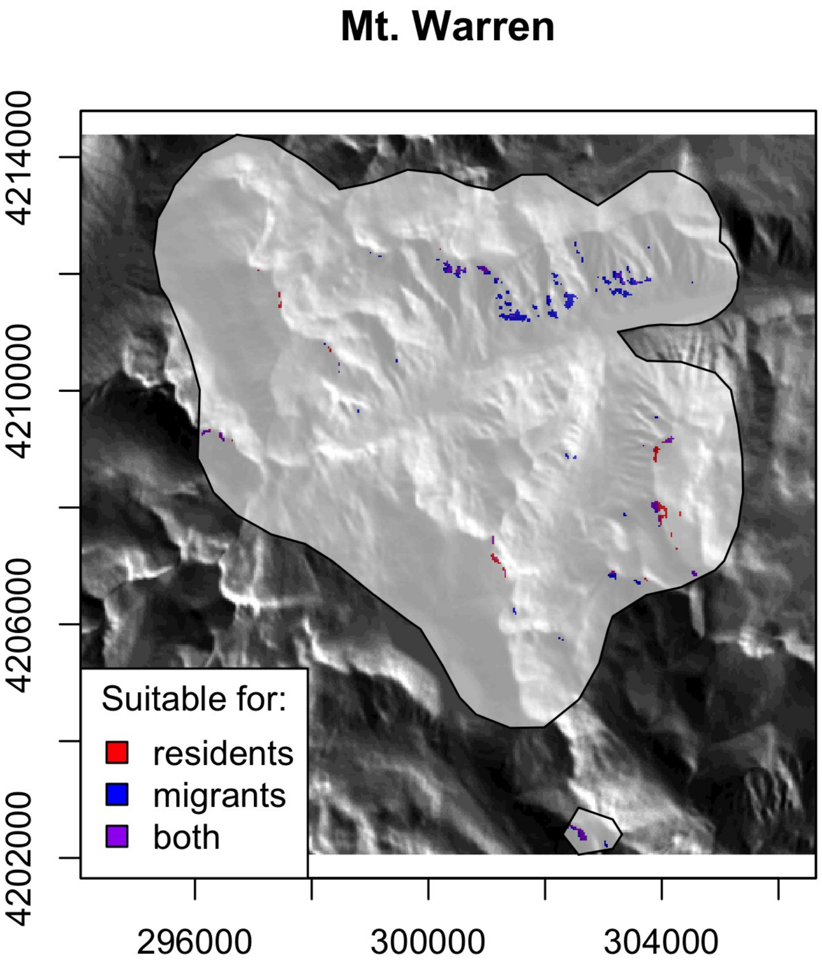
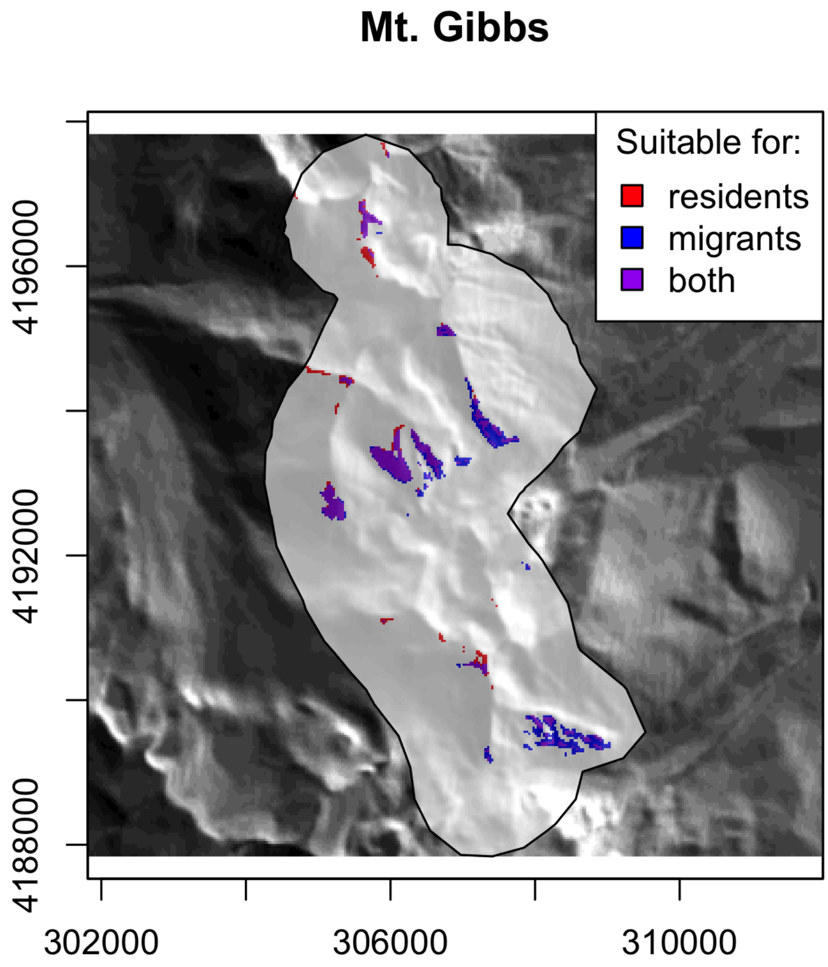


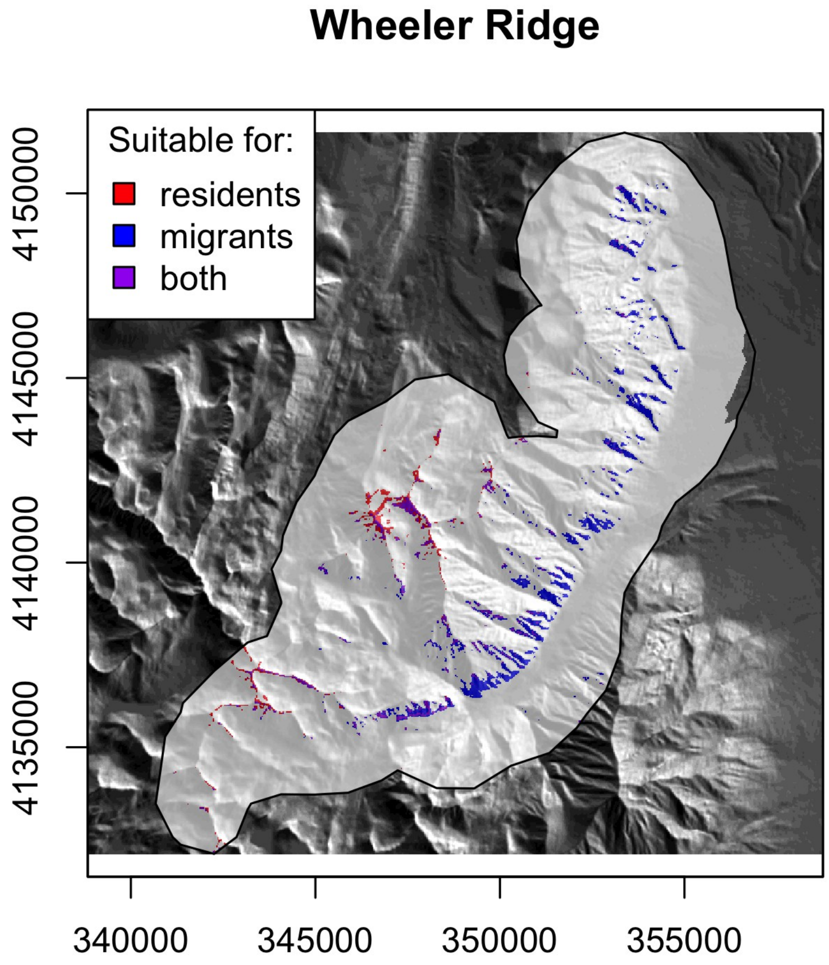
FIGURE 5-3. The probability of observing a Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) ewe with a lamb in spring as a function of age and migratory status. Ewes are more likely to be observed in summer with a lamb following residency than they are following migration.

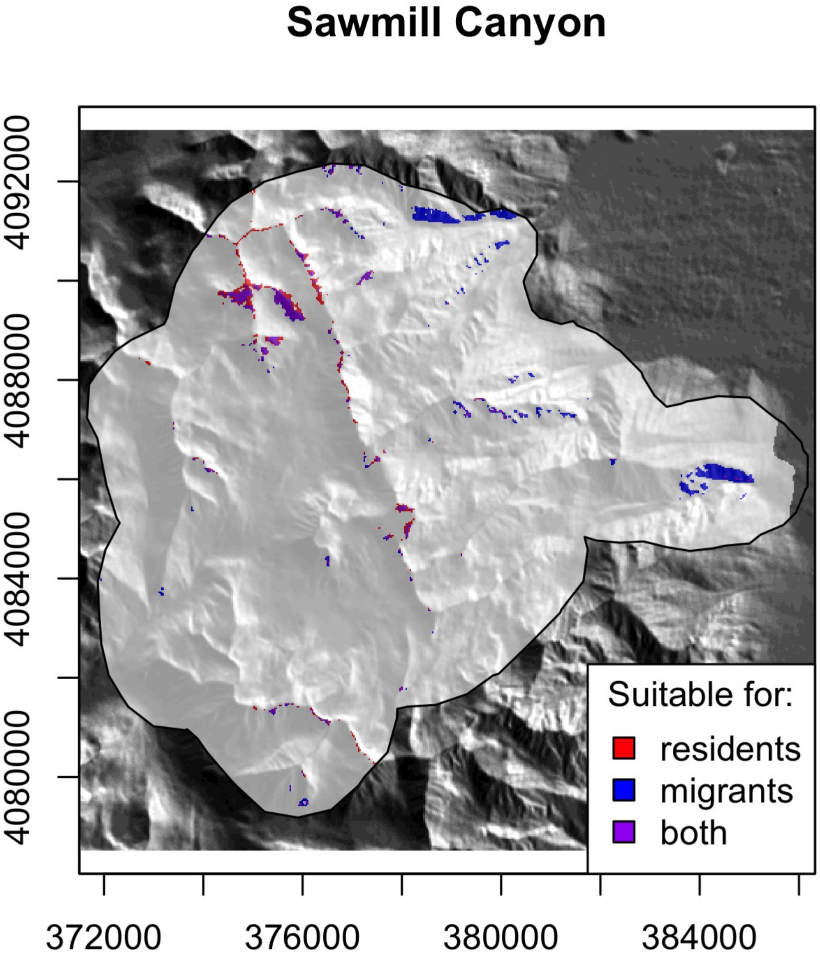


APPENDIX I. Areas predicted suitable for migrants, residents and both, by herd. Predictions shown are from scale-integrated RSF models (Chapter 4). Populations are ordered from north to south and predictions are plotted over hill shade to provide geographic context. X and Y axes show UTM coordinates.

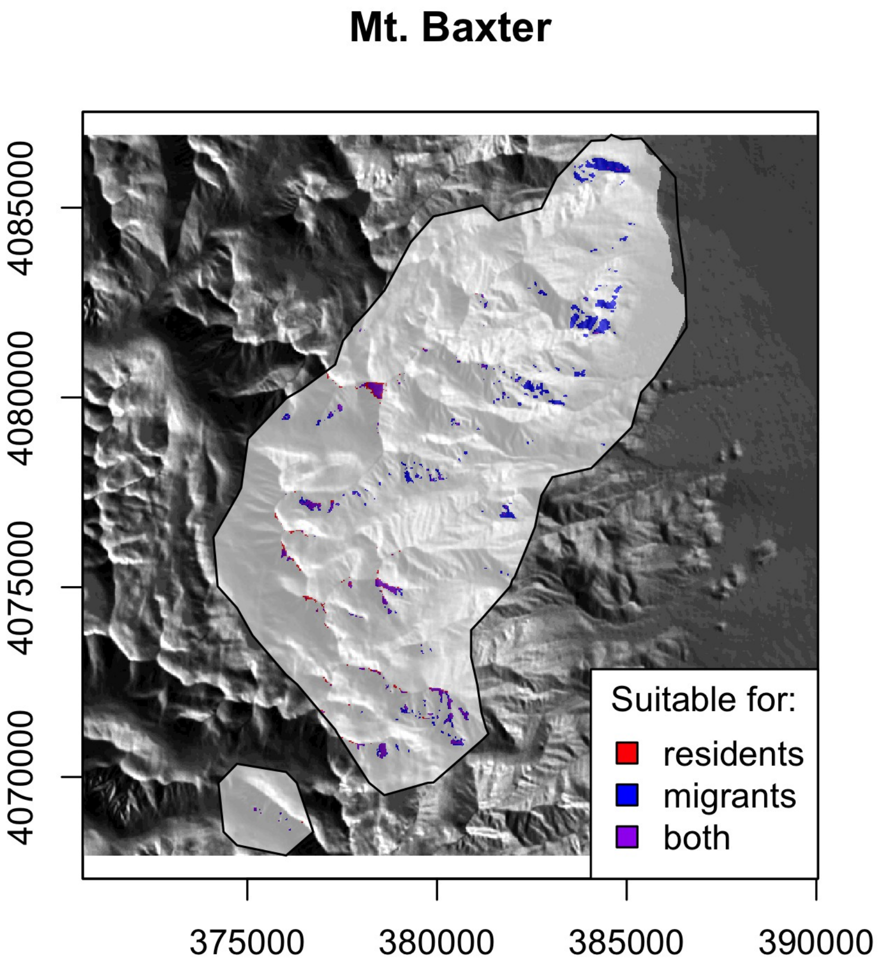


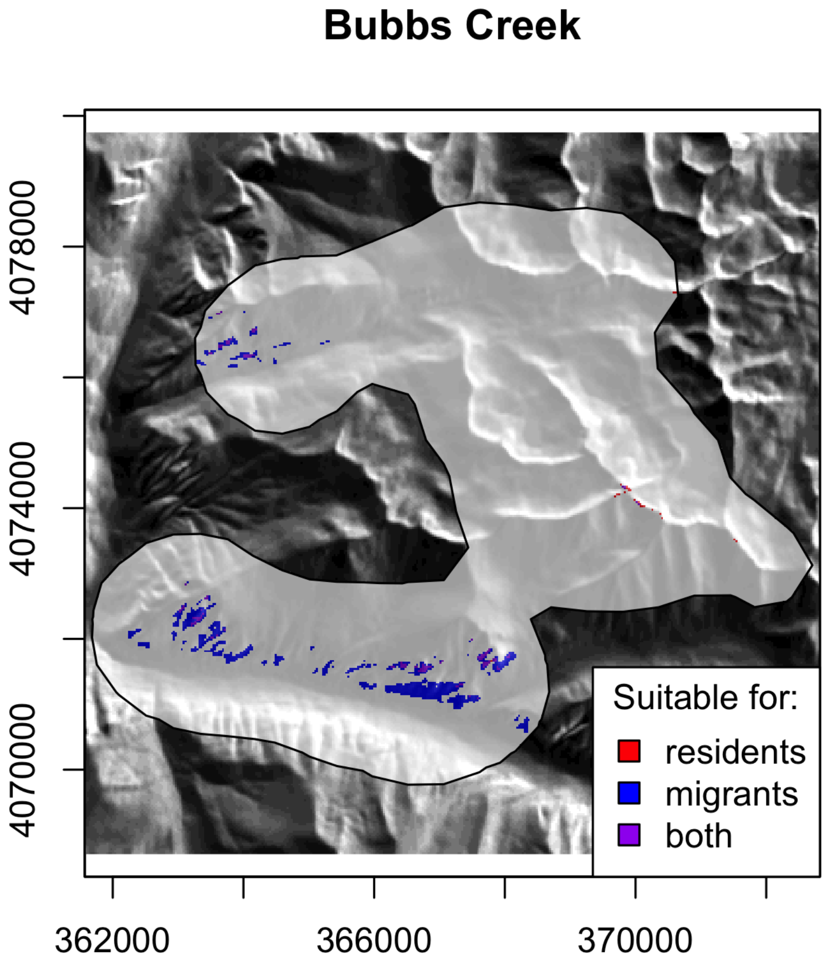

Mt. Gibbs
Suitable for:
residents
migrants
both
4196000
4192000
4188000
302000
306000
310000

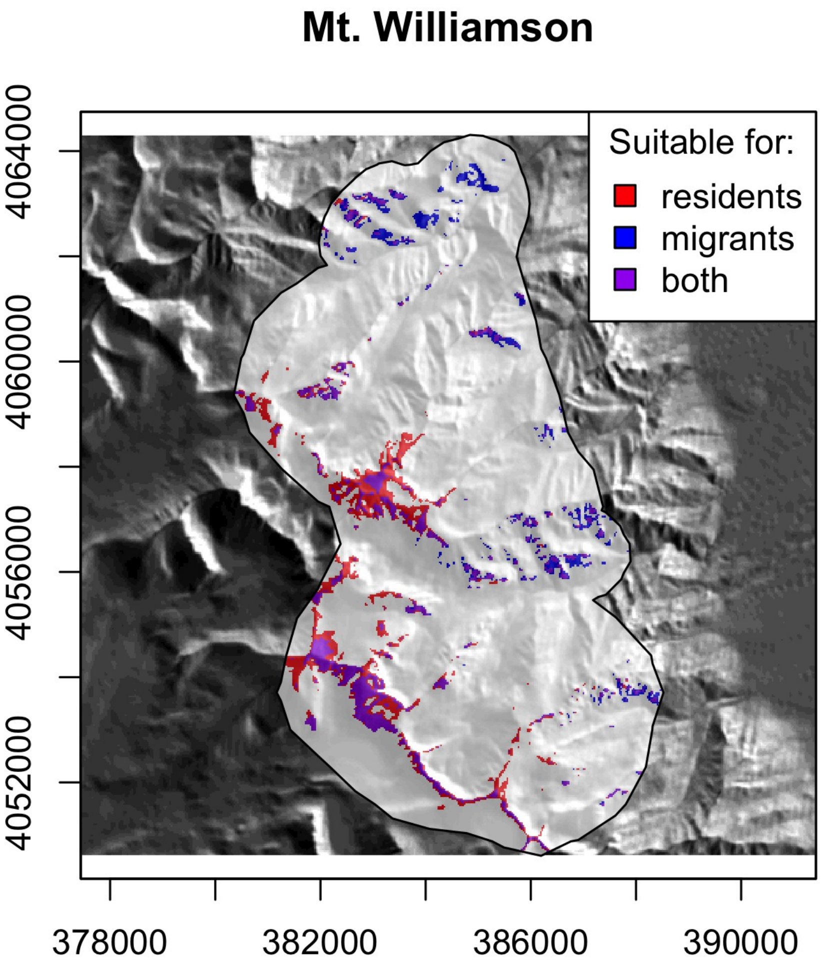

Wheeler Ridge
Suitable for:
residents
migrants
both
4150000
4145000
4140000
4135000
340000
345000
350000
355000

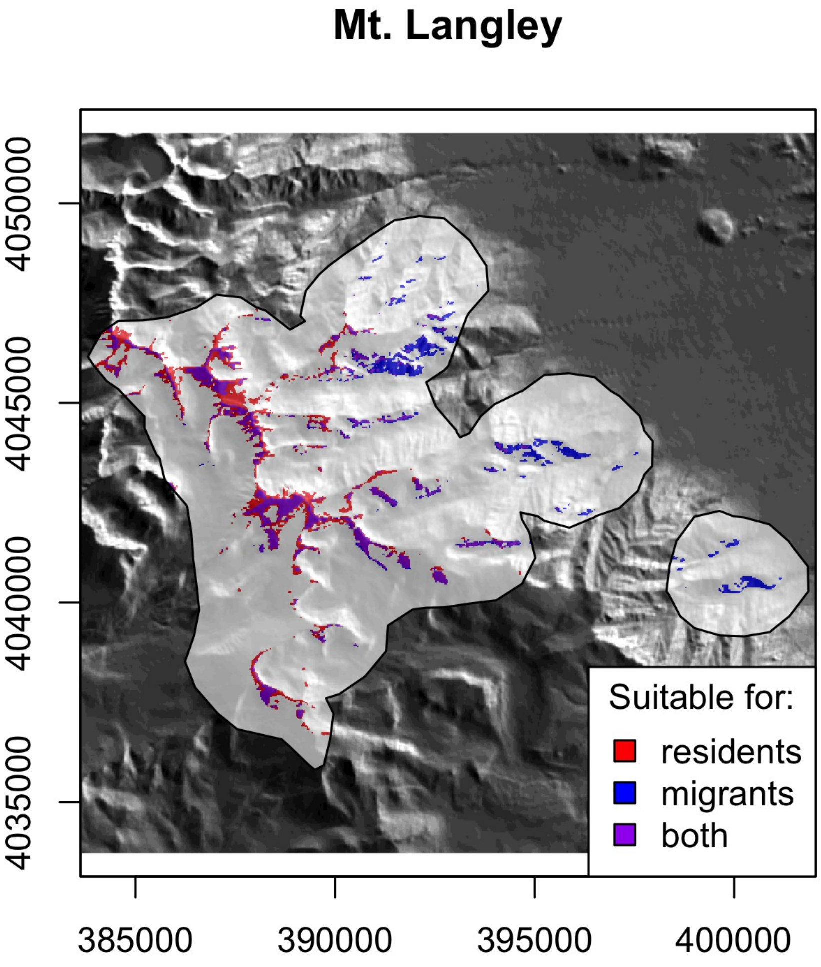


Sawmill Canyon
4092000
4088000
4084000
4080000
372000
376000
380000
384000
Suitable for:
🟥 residents
🟦 migrants
🟪 both


Mt. Baxter
4085000
4080000
4075000
4070000
375000
380000
385000
390000
Suitable for:
🟥 residents
🟦 migrants
🟪 both


Bubbs Creek
4078000
4074000
4070000
362000
366000
370000
Suitable for:
🟥 residents
🟦 migrants
🟪 both


Mt. Williamson
Suitable for:
🟥 residents
🟦 migrants
🟪 both
4064000
4060000
4056000
4052000
378000
382000
386000
390000


Mt. Langley
4050000
4045000
4040000
4035000
385000
390000
395000
400000
Suitable for:
residents
migrants
both