

Use Authorization

In presenting this thesis in partial fulfillment of the requirements for an advanced degree at Idaho State University, I agree that the Library shall make it freely available for inspection. I further state that permission to download and/or print my thesis for scholarly purposes may be granted by the Dean of the Graduate School, Dean of my academic division, or by the University Librarian. It is understood that any copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Signature _____

Date _____

ENVIRONMENTAL VARIATION, NOT RISK OF PREDATION, DRIVES THE
SPATIAL ECOLOGY OF SIERRA NEVADA BIGHORN SHEEP

by

Jeffrey Todd Villepique

A dissertation

submitted in partial fulfillment

of the requirements for the degree of

Doctor of Philosophy

in the Department of Biological Sciences

Idaho State University

May 2014

Copyright (2014) Jeffrey Todd Villepique

Committee Approval

To the Graduate Faculty:

The members of the committee appointed to examine the dissertation of Jeffrey Todd Villepique find it satisfactory and recommend that it be accepted.

R. Terry Bowyer,
Major Advisor

Vernon C. Bleich,
Committee Member

David J. Delehanty,
Committee Member

Charles R. Peterson,
Committee Member

Becky M Pierce,
Committee Member

David W. Rodgers,
Graduate Faculty Representative

Acknowledgments

I would like to express my gratitude to my advisor, Terry Bowyer, for the exceptional guidance, insight, encouragement, and hospitality throughout this endeavor. When obstacles arose, Terry was there with seemingly infinite creativity, knowledge, and experience to point the way and teach lessons on how good science may be used to surmount challenges. I want to thank my committee members who were mentors with the California Department of Fish and Wildlife, Vern Bleich and Becky Pierce, for giving me the opportunity to work for and learn from them and for being my advocate. Through Vern and Becky I was given the opportunity to work with Steve DeJesus, one of the most competent pilots ever to command a helicopter, and Tim Glenner, who along with Steve, taught me how to net-gun and work safely as a team to capture or count animals while keeping focus on the mission of coming back safely. Thanks also to committee members Chuck Peterson and Dave Delehanty, who provided valuable input on the study, in addition to encouragement and insights into the undertaking of doctoral research.

I want to thank my wife, Aleksandra, the first “Doctor Villepique,” who, in addition to lending her skill at C++ programming, provided unwavering support and encouragement.

Please see additional acknowledgments in Chapters I, II, and III.

Table of Contents

List of Figures	vii
List of Tables	ix
Abstract.....	xi
INTRODUCTION	1
CHAPTER I.....	5
Diet of Cougars (<i>Puma concolor</i>) following a decline in a population of mule deer (<i>Odocoileus hemionus</i>): lack of evidence for switching prey	
CHAPTER II.....	20
Evaluating GPS collar error: a critical evaluation of televilt POSREC-science™ collars and a method for screening location data.	
CHAPTER III.....	44
Resource selection by an endangered ungulate: a multiscale test of predator- induced range abandonment.	
APPENDIX I: Documentation for BADFIX Extension to ArcView 3.X.....	108
APPENDIX II: Avenue source code for BADFIX Extension to ArcView 3.X	111
APPENDIX III: C++ Source code for distance.c cluster selection program.....	117

List of Figures

CHAPTER I

- Figure 1. Locations where fecal samples of cougars (*Puma concolor*) were collected and ranges of mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) during winter (November–April) in the eastern Sierra Nevada, California18
- Figure 2. Mean proportions and 95% CIs of food items in diets of cougars (*Puma concolor*) as determined by analysis of feces in winter (November–April; $n = 178$) and summer (May–October; $n = 74$) 1991–1995, in the eastern Sierra Nevada, California 19

CHAPTER II

- Figure 1. All point locations (left) and movement path (right) generated from POSREC GPS collar deployed on mule deer RVD210, 10 Apr 2002–21 Sep 2002 38
- Figure 2. GPS collars deployed on a desert bighorn ewe D7 (POSREC; $n=852$ locations) and Sierra Nevada bighorn ewe S62 (Lotek GPS 4400s; $n=1035$ locations) and ram S18 (Televilt Simplex; $n=651$ locations) over the same period: 20 Mar – 8 Sep in 2004 (Posrec, Simplex) and 2005 (Lotek) 39
- Figure 3. Error distribution from fixed-location POSREC collars 40
- Figure 4. POSREC collar C600-175 tested under optimal sky visibility 41
- Figure 5. POSREC GPS collar movement path, mule deer RVD210, 10 Apr 2002–21 Sep 2002, generated from 3-D and better fixes 42
- Figure 6. POSREC GPS collar movement path, mule deer RVD210, 10 Apr 2002–21 Sep 2002, generated after screening all ≥ 2 -D fixes using the BadFix ArcView extension at the 50% probability level43

CHAPTER III

Figure 1. Landsat scene showing 95% composite home ranges (yellow) for Wheeler Ridge and Mt. Baxter winter ranges of bighorn sheep 99

Figure 2. Example of 2.4 km radius used to define available habitat for each GPS collar location in resource selection function (RSF) for Sierra Nevada Bighorn sheep, California, USA, 2002–2007 100

Figure 3. Hourly winter (January – April) movement rates by Sierra Nevada bighorn sheep, California, USA, 2002–2007 101

Figure 4. Annual precipitation and long-term mean (dashed horizontal line), Bishop, California, USA, 1987–2009 102

Figure 5. Representative winter habitat for Sierra Nevada bighorn sheep, illustrated by a portion of Wheeler Ridge from NAIP 2009 aerial image, indicating high elevation (>3,000 m) and low elevation (<2,000 m) habitat 103

Figure 6. Risk surface from probability density functions of active mountain lions (LNRISK), expressed as probability density (1–99), overlaid by locations where mountain lions were active, and locations where bighorn sheep were killed or cached by mountain lions, Sierra Nevada, California, USA, 2002–200 104

Figure 7. Odds ratios from resource selection functions (RSFs) for continuous predictor variables used in models of female and male Sierra Nevada bighorn sheep 105

Figure 8. Comparison of NDVI from Landsat TM in areas used by bighorn sheep in winter (January–April) at high elevations (>3000 m) and low elevations (<2000 m), in above average and below average precipitation years 106

Figure 9. Relationship between precipitation and NDVI tradeoff ($r^2 = 0.40$; $n = 51$) ... 107

List of Tables

CHAPTER I

Table 1. Percentage occurrence of food items in fecal samples of cougars (<i>Puma concolor</i>) in the eastern Sierra Nevada, California, during winter (November–April; $n = 178$) and summer (May–October; $n = 74$) 1991–1995	17
--------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------	----

CHAPTER II

Table 1. Percentile ^a location errors (m) for 8 GPS collar models and 1 handheld GPS unit with exceptional errors denoted by bold type	37
---------------------------------------------------------------------------------------------------------------------------------------------------------	----

CHAPTER III

Table 1. Hypotheses and general predictions regarding the influence of direct and indirect predation risk, forage availability, and tradeoff of forage at low versus high elevation on habitat selection relationship (+ or –), where relevant, for female and male Sierra Nevada bighorn sheep in the Sierra Nevada, California, USA, 2002–2007	93
Table 2. Model-averaged parameter estimates, 95% confidence intervals (CI), and Akaike importance weights (w_i) from models of RSF for female and male Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007	94
Table 3. Comparison of resource selection models incorporating risk surface from active mountain lions (LNRISK) with models substituting the correlated predictor elevation (ELEV), for female and male Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007	95

Table 4. Cross-validation results for resource-selection functions for female and male Sierra Nevada bighorn sheep, 2002–2007, indicating slope, coefficient of determination (r^2), and Spearman rank correlation (r_s), Sierra Nevada, California, USA, 2002–2007	96
Table A1. Description of candidate variables used to model resource selection by Sierra Nevada bighorn sheep and descriptive statistics for 18,240 random locations, Sierra Nevada, California, USA, 2002–2007	97
Table A2. Pearson correlation coefficients for candidate variables at 18,240 random locations used to model resource selection by Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007	98

Abstract

I investigated the spatial ecology of bighorn sheep (*Ovis canadensis sierrae*), an endangered taxon, in the eastern Sierra Nevada, California, USA, in relation to the activity of their primary predator, the mountain lion (*Puma concolor*), and to static and temporally varying conditions on their winter range. My co-authors and I also developed software utilities for screening GPS data.

I evaluated diet of mountain lions in 1991–1995, following a decline in mule deer (*Odocoileus hemionus*) and bighorn sheep populations, when mule deer remained <25% of prior numbers. Mule deer were the most frequent component in diets of mountain lions. Although most samples were collected <5 km from winter range of bighorn sheep, none contained evidence of bighorn. A single sample collected during summer contained bighorn sheep, indicating they were an unimportant component in diets of mountain lions.

I discovered implausible locations from POSREC-Science™ 600 series GPS collars deployed on mule deer and bighorn sheep, leading to a test of accuracy for those GPS collars. We documented unprecedented errors >2 km in 2% of fixes and >1 km in 12% of fixes. Data from six other GPS collar models showed POSREC collars to be uniquely inaccurate. I developed a method to identify outliers and an ArcView extension to screen GPS data and remove erroneous locations.

I investigated the influences of risk of predation by mountain lions, topographic ruggedness at multiple scales, and vegetation, land, and snow cover, on resource selection in winter by Sierra Nevada bighorn sheep. I hypothesized that those mountain ungulates would select areas with lower risk of predation and compared indices of forage quality in

drought versus wet years. Bighorn sheep selected areas of high solar radiation, where risk of predation by mountain lions was greatest, while mitigating indirect risk of predation by selecting for steep, rugged terrain. I demonstrated reduced benefit of migration to low elevation during drought years, when the difference in quality of forage was lower than in years of above-average precipitation. Evidence indicated that resources and environmental factors, and not predation, drove resource selection by Sierra Nevada bighorn sheep, and likely drove population declines.

INTRODUCTION

This investigation was initiated in response to a need to understand factors that contributed to the decline in numbers and subsequent listing of Sierra Nevada bighorn (*Ovis canadensis sierrae*) sheep as federally endangered (U.S. Fish and Wildlife Service, 2008). Past work by Wehausen (1996) attributed declines to behavioral responses by bighorn sheep to risk of predation by mountain lions. Consequently, the focus of this dissertation is on elucidating factors that may have driven a behavioral response by bighorn sheep to risk of predation by mountain lions during the period of population decline. This was accomplished by assessing available evidence from 1987–1995 when Wehausen (1996) hypothesized that bighorn sheep responded to predation risk by “range abandonment” and to investigating how bighorn sheep respond to risk of predation with contemporary data.

Three chapters herein contain differences in style, owing to different journal formatting requirements. All are written in the first-person plural, incorporating the contributions of my co-authors. Chapter I was published in the journal *Southwestern Naturalist* (Villemiquette et al. 2011) and Chapter II published in the journal *California Fish and Game* (Villemiquette et al. 2008). The third chapter is as a manuscript formatted in accordance with the open-access journal *Ecosphere*.

In Chapter I we investigated diets of mountain lions inferred from fecal samples collected during 1991–1995, a period overlapping declines in populations of Sierra Nevada bighorn sheep. Our goal was to assess evidence for a functional response by mountain lions to decreased numbers of mule deer, their primary prey, and detect prey-

switching (Logan and Sweanor, 2001; Rominger et al., 2004), and potential effects from direct predation on bighorn sheep.

Chapter II is an evaluation of location error in GPS collars, and presentation of a tool for performing triage to salvage reliable data and remove erroneous locations. This paper was an outgrowth of work on movement patterns of mule deer and bighorn sheep that was presented as an oral paper at the Western Section Annual Conference of The Wildlife Society, in January 2005 in Sacramento, California, USA. That work reported negative results of attempts to correlate movement vectors from GPS collars on bighorn sheep with proximity of mountain lions, also fitted with GPS collars. No pattern could be elucidated to show changes in movements of bighorn sheep in response to proximity of mountain lions, a result that receives support in later work presented in Chapter III. Further investigation of movement vectors measured by GPS collars on bighorn sheep and mule deer uncovered implausible results from a particular model of GPS collar deployed on 44 mule deer, and 7 desert bighorn sheep, which fortunately was not used on Sierra Nevada bighorn sheep. Chapter III documents quantification of errors and development of a logistic model to identify likely erroneous fixes, which was made into an ArcView3.X extension (Appendices I and II).

Chapter III investigated factors driving habitat selection by Sierra Nevada bighorn sheep under risk of predation with a resource-selection function (RSF; Manly et al. 2002, Boyce et al. 2002), and an information theoretic approach to assess support of competing models (Burnham and Anderson 2002). Modeling employed data collected from two populations of bighorn sheep over 5 years with highly variable precipitation, yielding RSF models of broad applicability. Intensive monitoring of GPS-collared mountain lions

allowed us to locate bighorn sheep killed by mountain lions. We evaluated patterns of movement from GPS collars deployed on mountain lions with a C++ program (Appendix III) to identify locations characteristic of resting and feeding sites, allowing a probability density function to be generated from remaining locations and representing a risk surface where mountain lions were active and likely hunting. We employed satellite data in RSF models to investigate responses of GPS-collared animals to remotely sensed characteristics, as well as to determine what those remotely sensed measures can tell about conditions during the historical period of range abandonment by Sierra Nevada bighorn sheep (Wehausen 1996).

Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* 146:112-134.

Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281-300.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.

Logan, K. A. , and L. L. Swenar. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, New York, New York, USA.

- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer, Dordrecht, The Netherlands.
- Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993-999.
- U.S. Fish and Wildlife Service. 2008. Recovery plan for the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Villepique, J. T., V. C. Bleich, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of televilt POSREC-science™ collars and a method for screening location data. *California Fish and Game* 94:155-168.
- Villepique, J. T., B. M. Pierce, V. C. Bleich, and R. T. Bowyer. 2011. Diet of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey. *The Southwestern Naturalist* 56:187–192.
- 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.

CHAPTER I.

Diet of Cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey

ABSTRACT—We investigated diet of cougars (*Puma concolor*) in the eastern Sierra Nevada, California, following a decline in the population of mule deer (*Odocoileus hemionus*). Mule deer declined 84% from 1985 to 1991, a period concurrent with declines in bighorn sheep (*Ovis canadensis sierrae*; an endangered taxon). An index to numbers of cougars lagged behind those declines, with a reduction of ca. 50% during 1992–1996. We determined diet of cougars by analysis of fecal samples collected during 1991–1995, when the population of mule deer was <25% of its former size. Mule deer was in 79% of 178 feces in winter and 58% of 74 feces in summer. Although most (69%) fecal samples in winter were <5 km from, or within, (25%) winter range of bighorn sheep, none contained evidence of bighorn sheep. One fecal sample in summer contained remains of bighorn sheep, indicating that those ungulates were not an important component of the diet during our investigation.

Mule deer (*Odocoileus hemionus*) are the primary prey of cougars (*Puma concolor*) in the Great Basin (Pierce et al., 1999, 2000a). Cougars select prey based upon size or sex (Pierce et al., 2000b), and can respond to declines of prey by switching to alternative prey (Logan and Sweanor, 2001; Rominger et al., 2004). We studied diets of cougars reconstructed from fecal samples collected following a decline in populations of mule deer (Bowyer et al. 2005) and bighorn sheep (*Ovis canadensis*; Wehausen 1996) in

a Great Basin ecosystem. We hypothesized that occurrence of mule deer in diets of cougars would be more common when mule deer were concentrated on winter range than during summer, when alternative prey were expected to occur more frequently. We further postulated that the decline and persistent low populations of mule deer would cause cougars to consume alternative prey, including domestic animals and bighorn sheep, throughout the year.

MATERIALS AND METHODS—Round Valley, Inyo and Mono counties, California, at the eastern base of the Sierra Nevada (37°25'N, 118°37'W), was the winter range for a herd of migratory mule deer (Kucera, 1992). Predominant vegetation in Round Valley was big sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*), characteristic of the Great Basin series described by Storer and Usinger (1968). Elevations ranged from 1,300 m at the valley floor to >3,500 m at Wheeler Ridge and Mount Tom, which bound the valley to the north and west, respectively. Further description of this ecosystem is available from long-term studies of predator-prey interactions (Pierce et al., 2000b, 2004; Bowyer et al., 2005). Minimum number of mule deer occupying Round Valley during winter declined by 84%, from 5,978 in 1985 to 939 in 1991; annual surveys indicated the population remained between 900 and 1,400 during 1991–1995 (Bowyer et al., 2005). Bighorn sheep experienced a concurrent decline in populations from the late 1980s through early 1990s, which was attributed in part to responses by bighorn sheep to predation by cougars (Wehausen, 1996). This subspecies of bighorn sheep (*Ovis canadensis sierrae*) is an endangered taxon (United States Fish and Wildlife Service, 2008). Decreases in an index to abundance of cougars lagged

behind declines in populations of mule deer with a reduction of ca. 50% during 1992–1996 (Pierce et al., 2000a).

We collected recently deposited feces of cougars when located by researchers or hounds in the course of trailing cougars during 1991–1995 (Pierce, 2000a). Feces often were associated with kill sites or latrines (locations used repeatedly for scent marking; Pierce et al., 2000b). Most (94%) fecal samples were <14 days old. Food items were determined from remains of bone, teeth, and claws, and from hair examined for color, length, thickness, and medullary and cuticular characteristics (Mayer, 1952; Bowyer et al., 1983). Samples were analyzed by Big Sky Laboratories (Florence, Montana) and food items were determined with dichotomous keys (Moore et al., 1974; Kennedy and Carbyn, 1981) and an extensive reference collection of hairs, teeth, and bones.

Taxa identified from fecal samples were grouped into five categories: mule deer, bighorn sheep, leporids, livestock and pets, and small animals or other materials. We calculated percentage occurrence for each category and *SE* and confidence intervals (*CI*) for proportions (Bowden et al., 1984; Bowyer, 1991). Samples were analyzed by comparing 95% *CI*s from a binomial distribution, an approach that was especially appropriate because it allows sampling with replacement, and does not assume independence of samples (Zar, 1999). We interpreted lack of overlap in 95% *CI*s as indicative of statistically significant differences. Data were grouped into 2 seasons, winter (November–April) and summer (May–October), based on dates when mule deer typically migrated to winter range (Kucera, 1992; Pierce et al., 1999).

We used ArcGIS Desktop 9.2 (Environmental Systems Research Institute, Redlands, California) to generate a point layer of locations from Universal Transverse

Mercator coordinates where samples of feces were collected. Limited data were available for locations of mule deer and bighorn sheep during 1991–1995, when fecal samples of cougars were collected. In absence of concurrent information, we used data from global positioning system (GPS) collars deployed on mule deer and bighorn sheep during 2002–2007 to define winter ranges for those taxa (Krausman et al., 2004; Villepique et al., 2008). Although some locations of mule deer were documented concurrently with our study (Pierce et al., 2004), similar data for bighorn sheep were unavailable because 1986 was the last year that telemetry collars were deployed on bighorn sheep in the study area until 1999 (K. Jones, pers. comm.). We believe locations of bighorn sheep from GPS collars to be representative of distributions in 1991–1995 because those locations are consistent with previous studies (Andaloro and Ramey, 1981) that, like contemporary data, indicated use of both high and low elevations by bighorn sheep in winter (T. Stephenson, pers. comm.).

We used Home Range Tools for ArcGIS (Rodgers et al., 2005) to derive size of home ranges using the 95% adaptive-kernel method for bighorn sheep and for mule deer in winter (November–April). Polygons for range in winter were defined with GPS locations from 26 bighorn sheep (7 males, 19 females) and 37 female mule deer during 2002–2007, rarified to one randomly selected location per week, and employing a smoothing factor of 80% h_{ref} (Worton, 1995). Elevations were derived from a 1:24,000-scale, 10-m-digital model for elevation (United States Geological Survey, <http://seamless.usgs.gov>).

RESULTS—One fecal sample contained feathers from an unidentified bird, but remains of mammals occurred in >99% of samples. Mule deer was the most frequent food in diets of cougars and occurred in $79.2 \pm 4.7\%$ (*SE*) of fecal samples in winter ($n = 178$) and $58.1 \pm 5.7\%$ of samples during summer ($n = 74$; Table 1). Leporids were the second most common food in both seasons (Table 1). Use of mule deer was significantly greater in winter compared with summer, but no significant difference between seasons was evident in other categories of diet. We detected no evidence of increased occurrence of domestic animals in fecal samples during summer, despite a higher proportion of depredation permits issued for cougars preying on domestic animals in summer ($70.6 \pm 7.6\%$) compared to winter ($29.4 \pm 11.8\%$; M. Kepner, pers. comm.). Samples in winter were at lower elevations ($1,833 \pm 23.0$ m) than samples in summer ($2,078 \pm 32.6$ m). Most (85.4%) fecal samples collected in winter were <5 km from, or within (56.7%), the winter range of mule deer, whereas 69.1% of fecal samples in winter were <5 km from, or within (24.7%), winter range of bighorn sheep. One sample, collected on 3 July 1993, contained remains of bighorn sheep. This sample was 7.7 km from the home range of bighorn sheep, a radius that encompassed 63.8% of all fecal samples. No evidence of bighorn sheep occurred in 44 fecal samples collected during winter within the polygon for winter range of bighorn sheep.

DISCUSSION—Mule deer occurred most frequently in diets of cougars when deer were concentrated on winter range, consistent with our predictions. Despite the massive decline in the population of mule deer immediately prior to our study, little evidence existed to support prey-switching by cougars to bighorn sheep, as that taxon was detected

in one fecal sample. Although bighorn sheep were available, they were not an important component in diets of cougars.

Several potential problems exist in interpreting diets from remains of prey in feces (Bowyer et al., 1983). We collected fecal samples of cougars opportunistically where the same individual likely contributed more than one sample; however, we used the method of Bowden et al. (1984), which has no associated requirement for independence of samples, to calculate confidence intervals for proportions. We could not eliminate the possibility that samples over represented individual cougars because most (85.3%) fecal samples were from unknown individuals; however, 14.7% of samples were produced by 17 marked cougars. Our allocation of sampling effort thus encompassed a minimum of 17 individuals and likely constituted a representative sample of cougars in our study area. Additionally, hounds were used to locate many fecal samples, and species of prey could be overrepresented at kill sites. Nevertheless, any potential biases should be minimal, because hounds are proficient at locating carcasses of domestic animals, as well as bighorn sheep and mule deer.

We could not distinguish between prey killed by cougars from food that might have been obtained by scavenging (Bauer et al., 2005). Similarly, the occurrence of hair from cougars in 27.8% of fecal samples likely resulted predominantly from grooming, although some occurrences could have resulted from consumption of conspecifics (Galentine and Swift, 2007). Inferring diet from fecal samples could be confounded by differential digestibility of prey, but our hypotheses relate primarily to the occurrence of large mammals. Consequently, bias in the inferred diets of cougars should be minimal with respect to mule deer and bighorn sheep. Further, remains of prey in feces of

carnivores have been used successfully to track mortality of young mule deer (Bowyer, 1987), and likely provide a reliable index to use of prey by cougars among seasons. Mule deer were more available to cougars when deer were concentrated on winter range (Kucera, 1992; Pierce et al., 2004), an area of ca. 120 km², than during summer, when deer were dispersed over a much larger area (ca. 2,500 km²). Thus, cougars showed a functional response to the concentration of mule deer on winter range, as evidenced by increased frequency of remains of deer in their feces during winter. We were surprised that no concomitant increase in frequency of alternative prey, such as livestock and pets, was evident during summer. Despite the response to seasonal availability of primary prey, cougars did not respond strongly to the long-term decline in mule deer by switching to bighorn sheep. Several investigators have documented predation by cougars on bighorn sheep (Ross et al., 1997; Hayes et al., 2000; Festa-Bianchet et al., 2006), and others have suggested that increased predation on bighorn sheep can be attributed to a switch to alternate prey by cougars faced with declines in their primary prey (Kamler et al., 2002; Rosas-Rosas et al., 2003; Rominger et al., 2004). Although our study occurred under conditions of a large decline in the population of mule deer, no fecal samples of cougars collected on or adjacent to the winter range of bighorn sheep contained evidence of feeding on that ungulate; instead the one sample containing bighorn sheep was found in July, 7.7 km from the range of bighorn sheep. These results suggest that, in contrast to prevailing theory (Sawyer and Lindzey, 2002), bighorn sheep may not always experience elevated predation by cougars following a precipitous decline in populations of mule deer.

Determining extent of predation by cougars on bighorn sheep in the Sierra Nevada is critically important to efforts to conserve that endangered taxon (United States Fish and Wildlife Service, 2008), and results could aid in conservation of bighorn sheep elsewhere. Wehausen (1996) posited that bighorn sheep abandoned use of winter range at Mount Baxter in response to the risk of predation and concluded that similar behavioral changes were important in the decline of bighorn sheep throughout the Sierra Nevada. Despite a decline in the population of mule deer to <25% of its former size, and examination of diets of cougars over multiple years, we were unsuccessful in our attempt to establish bighorn sheep as an important item in the diet of those large carnivores. Thus, the mechanism for abandonment of winter range by bighorn sheep remains unclear and more research is necessary to fully understand factors related to the decline of those endangered ungulates.

We thank houndsmen J. L. Davis and J. W. Ostergard, and others, including W. J. Allsup, C. S. Baker, C.-L. Chetkiewicz, V. L. Davis, P. E. Partridge, G. Raygorodetsky, D. C. Stoner, and J. D. Wehausen for assistance in tracking cougars and in collecting samples, and A. J. Howell for assistance with the manuscript. This study was supported by the California Department of Fish and Game Deer Herd Management Improvement Program, California Department of Fish and Game Sierra Nevada Bighorn Sheep Recovery Program, California Deer Association, and Department of Biological Sciences at Idaho State University. This is a contribution from the Sierra Nevada Bighorn Sheep Recovery Program and is professional paper 076 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- ANDALORO, L., AND R. R. RAMEY. 1981. The relocation of bighorn sheep in the Sierra Nevada of California. University of California, Santa Cruz, Environmental Field Program Publication 7:1-60.
- BAUER, J. W., K. A. LOGAN, L. L. SWEANOR, AND W. M. BOYCE. 2005. Scavenging behavior in puma. *Southwestern Naturalist* 50:466-471.
- BOWDEN, D. C., A. E. ANDERSON, AND D. E. MEDIN. 1984. Sampling plans for mule deer sex and age ratios. *Journal of Wildlife Management* 48:500-509.
- BOWYER, R. T. 1987. Coyote group size relative to predation on mule deer. *Mammalia* 51:515-526.
- BOWYER, R. T. 1991. Timing of parturition and lactation in southern mule deer. *Journal of Mammalogy* 72:138-145.
- BOWYER, R. T., S. A. MCKENNA, AND M. E. SHEA. 1983. Seasonal changes in coyote food habits as determined by fecal analysis. *American Midland Naturalist* 109:266-273.
- BOWYER, R. T., D. K. PERSON, AND B. M. PIERCE. 2005. Detecting top-down versus bottom-up regulation of ungulates by large carnivores: implications for conservation of biodiversity. Pages 342-361 in *Large carnivores and the conservation of biodiversity* (J. C. Ray, K. H. Redford, R. S. Steneck, and J. Berger, editors). Island Press, Covelo, California.
- FESTA-BIANCHET, M., T. COULSON, J. M. GAILLARD, J. T. HOGG, AND F. PELLETIER. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* 273:1537-1543.

- GALENTINE, S. P., AND P. K. SWIFT. 2007. Intraspecific killing among mountain lions (*Puma concolor*). *Southwestern Naturalist* 52:161-164.
- HAYES, C. L., E. S. RUBIN, M. C. JORGENSEN, R. A. BOTTA, AND W. M. BOYCE. 2000. Mountain lion predation of bighorn sheep in the peninsular ranges, California. *Journal of Wildlife Management* 64:954-959.
- KAMLER, J. F., R. M. LEE, J. C. DEVOS, W. B. BALLARD, AND H. A. WHITLAW. 2002. Survival and cougar predation of translocated bighorn sheep in Arizona. *Journal of Wildlife Management* 66:1267-1272.
- KENNEDY, A. J., AND L. N. CARBYN. 1981. Identification of wolf prey using hair and feather remains with special reference to western Canadian national parks. Canadian Wildlife Service, Edmonton, Alberta, Canada.
- KRAUSMAN, P. R., V. C. BLEICH, J. W. CAIN, T. R. STEPHENSON, D. W. DEYOUNG, P. W. MCGRATH, P. K. SWIFT, B. M. PIERCE, AND B. D. JANSEN. 2004. Neck lesions in ungulates from collars incorporating satellite technology. *Wildlife Society Bulletin* 32:987-991.
- KUCERA, T. E. 1992. Influences of sex and weather on migration of mule deer in California. *Great Basin Naturalist* 52:122-130.
- LOGAN, K. A., AND L. L. SWEANOR. 2001. Desert puma: evolutionary ecology and conservation of an enduring carnivore. Island Press, New York.
- MAYER, W. V. 1952. The hair of California mammals with keys to the dorsal guard hairs of California mammals. *American Midland Naturalist* 48:480-512.

- MOORE, T. D., L. E. SPENCE, AND C. E. DUGNOLLE. 1974. Identification of dorsal guard hairs of some mammals of Wyoming. Wyoming Game and Fish Department Bulletin 14:1-177.
- PIERCE, B. M., V. C. BLEICH, AND R. T. BOWYER. 2000a. Social organization of mountain lions: does a land-tenure system regulate population size? Ecology 81:1533-1543.
- PIERCE, B. M., V. C. BLEICH, AND R. T. BOWYER. 2000b. Selection of mule deer by mountain lions and coyotes: effects of hunting style, body size, and reproductive status. Journal of Mammalogy 81:462-472.
- PIERCE, B. M., V. C. BLEICH, AND J. D. WEHAUSEN. 1999. Migratory patterns of mountain lions: implications for social regulation and conservation. Journal of Mammalogy 80:986-992.
- PIERCE, B. M., R. T. BOWYER, AND V. C. BLEICH. 2004. Habitat selection by mule deer: forage benefits or risk of predation? Journal of Wildlife Management 68:533-541.
- RODGERS, A. R., A. P. CARR, L. SMITH, AND J. G. KIE. 2005. HRT: home range tools for ArcGIS®. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research, Thunder Bay, Ontario, Canada
- ROMINGER, E. M., H. A. WHITLAW, D. L. WEYBRIGHT, W. C. DUNN, AND W. B. BALLARD. 2004. The influence of mountain lion predation on bighorn sheep translocations. Journal of Wildlife Management 68:993-999.
- ROSAS-ROSAS, O. C., R. VALDEZ, L. C. BENDER, AND D. DANIEL. 2003. Food habits of pumas in northwestern Sonora, Mexico. Wildlife Society Bulletin 31:528-535.

- ROSS, P. I., M. G. JALKOTZY, AND M. FESTABIANCHET. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Canadian Journal of Zoology* 75:771-775.
- SAWYER, H., AND F. LINDZEY. 2002. A review of predation on bighorn sheep (*Ovis canadensis*). Wyoming Cooperative Fish and Wildlife Research Unit, Laramie.
- STORER, T. I., AND R. L. USINGER. 1968. Sierra Nevada natural history. University of California Press, Berkeley.
- UNITED STATES FISH AND WILDLIFE SERVICE. 2008. Recovery plan for the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*). United States Fish and Wildlife Service, Portland, Oregon.
- VILLEPIQUE, J. T., V. C. BLEICH, R. A. BOTTA, B. M. PIERCE, T. R. STEPHENSON, AND R. T. BOWYER. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-science™ collars and a method for screening location data. *California Fish and Game* 94:155-168.
- 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.
- WORTON, B. J. 1995. Using Monte Carlo simulation to evaluate kernel-based home range estimators. *Journal of Wildlife Management* 59:794-800.
- ZAR, J. H. 1999. Biostatistical analysis. Prentice Hall, Upper Saddle River, New Jersey.

TABLE 1—Percentage occurrence of food items in fecal samples of cougars (*Puma concolor*) in the eastern Sierra Nevada, California, during winter (November–April; $n = 178$) and summer (May–October; $n = 74$) 1991–1995.

Food item	Season	
	Winter	Summer
Mule deer (<i>Odocoileus hemionus</i>)	79.2	58.1
Cougar (<i>Puma concolor</i>)	27.0	29.7
Unidentified	9.0	16.2
Black-tailed jackrabbit (<i>Lepus californicus</i>)	9.0	5.4
Unidentified vegetation	4.5	0
Dog (<i>Canis familiaris</i>)	4.0	5.4
Desert cottontail (<i>Sylvilagus audubonii</i>)	3.9	2.7
Goat (<i>Capra hircus</i>)	3.4	5.4
Desert woodrat (<i>Neotoma lepida</i>)	3.4	0
Ground squirrel (<i>Spermophilus</i>)	2.2	5.4
Grass	2.2	1.4
Bobcat (<i>Lynx rufus</i>)	1.7	0
Vole (<i>Microtus</i>)	1.1	2.7
Unidentified rodent	1.1	2.7
Cat (<i>Felis catus</i>)	1.1	0
Deermouse (<i>Peromyscus</i>)	0.6	6.8
Common muskrat (<i>Ondatra zibethicus</i>)	0.6	0
Western spotted skunk (<i>Spilogale gracilis</i>)	0.6	0
Unidentified bird	0.1	0
American badger (<i>Taxidea taxus</i>)	0	2.7
Sheep (<i>Ovis aries</i>)	0	2.7
Jumping mouse (<i>Zapus</i>)	0	1.4
Long-tailed weasel (<i>Mustela frenata</i>)	0	1.4
Bighorn sheep (<i>Ovis canadensis sierrae</i>)	0	1.4
Yellow-bellied marmot (<i>Marmota flaviventris</i>)	0	1.4
House mouse (<i>Mus musculus</i>)	0	1.4
Coyote (<i>Canis latrans</i>)	0	1.4
Unidentified carnivore	0	1.4
Insects	0	1.4

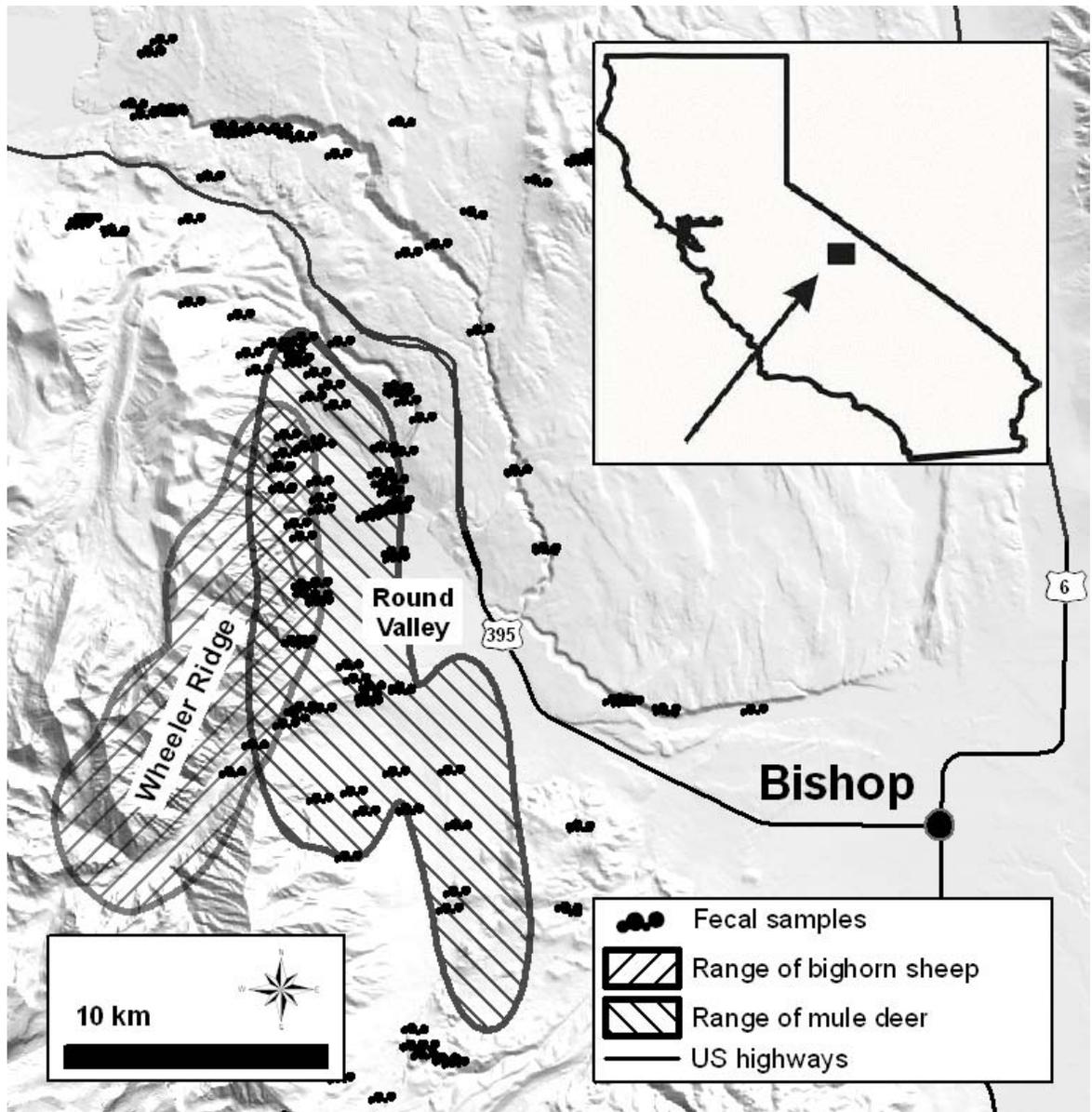


FIG. 1—Locations where fecal samples of cougars (*Puma concolor*) were collected and ranges of mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) during winter (November–April) in the eastern Sierra Nevada, California.

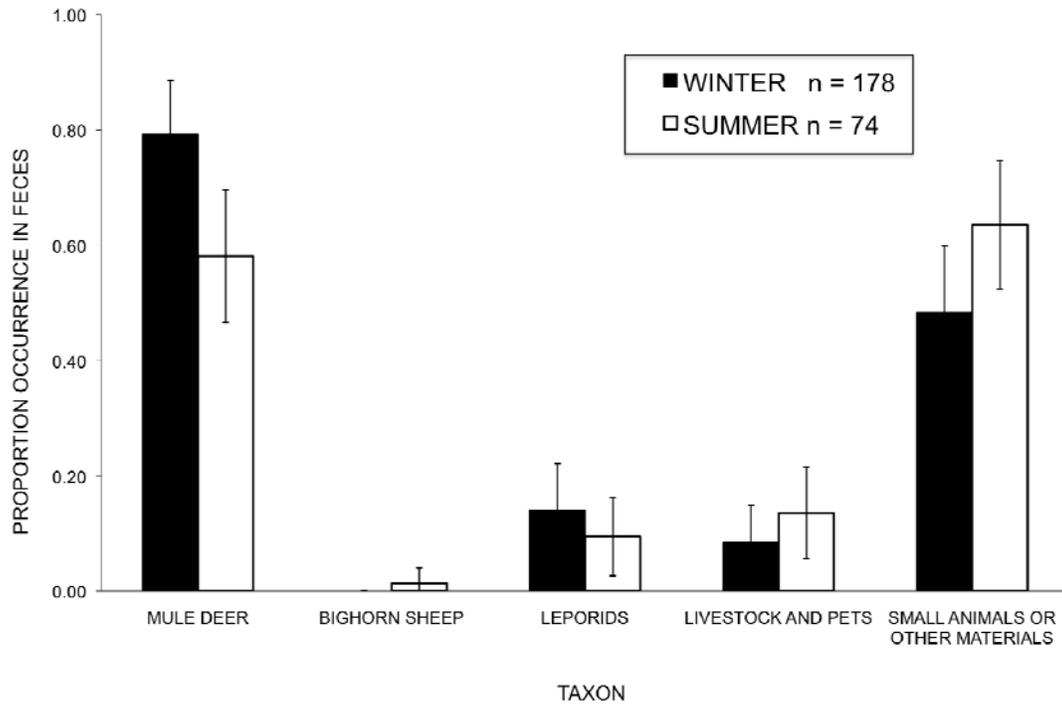


FIG. 2—Mean proportions and 95% CIs of food items in diets of cougars (*Puma concolor*) as determined by analysis of feces in winter (November–April; $n = 178$) and summer (May–October; $n = 74$) 1991–1995, in the eastern Sierra Nevada, California.

CHAPTER II.

Evaluating GPS collar error: a critical evaluation of televilt POSREC-science™ collars and a method for screening location data.

Wildlife telemetry collars incorporating Global Positioning System (GPS) units are thought to provide accurate locations when the GPS receiver obtains an adequate sky view. We deployed 32 POSREC-Science™ 600 series 12-channel GPS collars (Televilt/TVP Positioning AB, Lindesberg, Sweden) on mule deer (*Odocoileus hemionus*) and bighorn sheep (*Ovis canadensis*) in 3 California mountain ranges from 2002 to 2005. Evaluation of data from those deployments showed numerous implausible movements, which lead us to question the accuracy of POSREC GPS collars. Because of the questionable data encountered, we tested the precision of Televilt POSREC-Science™ 600 collars under several conditions: 1) an area of optimal sky visibility; 2) *ad hoc* test locations where collars remained attached to deceased mule deer prior to recovery of the collar; and 3) *ad hoc* test locations inside a 1-floor, wood-framed building, or outside the homes of 2 biologists, for a total of 663 GPS positions. Unprecedented errors in excess of 2 km occurred in 2% of fixes, whereas 12% of fixes were >1 km and 53% > 100 m from the true location. Comparisons among 6 additional GPS collar models from 3 manufacturers showed POSREC collars to be unique in their lack of precision. Because viewing point data alone may belie the presence of flawed GPS fixes, we urge researchers using GPS collars, particularly Televilt POSREC collars, to evaluate patterns of movement to ensure that data are not affected by sampling artifacts. We developed a method for screening GPS collar data and provide an ArcView

extension useful for removing erroneous fixes. We suggest researchers contemplating purchases of GPS collars obtain test data from the individual collars they will deploy, to ensure that real-world precision meets study objectives.

INTRODUCTION

Studies of GPS accuracy have evaluated effects of canopy and terrain (Rempel et al. 1995, Dussault et al. 1999, D'Eon et al. 2002, Di Orio et al. 2003, Cain et al. 2005, DeCesare et al. 2005) as well as collar orientation (Moen et al. 1996, D'Eon and Delporte 2005). These studies elucidated external influences on location accuracy, and have important implications for the interpretation of data from GPS collars (D'Eon 2003, Frair et al. 2004). These comparisons of accuracy in commercially available GPS collars, however, have been limited to collars made by Advanced Telemetry Systems (ATS; Isanti, Minnesota), Lotek Wireless (Newmarket, Ontario), and Telonics, Inc. (Mesa, Arizona). Frair et al. (2004) and Gau et al. (2004) provided data on respective fix rates and reliability of Televilt GPS-Simplex™ collars, but did not assess accuracy or precision. This work documents the unprecedented magnitude of location errors inherent in widely deployed Televilt POSREC-Science™ GPS collars.

Evaluation of GPS collar error was not a planned objective of our studies, but when extraordinarily improbable position data were detected after deploying collars on study animals, we sought data from collars at fixed locations to verify the presence of errors. To this end, we combined controlled testing with opportunistic data from fixed locations identified retrospectively from a database of GPS collar fixes, yielding data from several GPS collar models under a range of satellite visibility conditions and illuminating the prevalence of heretofore unprecedented errors. We also provide a

method that is broadly applicable to screening GPS collar data for patterns characteristic of flawed locations.

METHODS

Our methodology emanated in response to conspicuous problems with data obtained from deployment of POSREC GPS collars and our need to quantify apparent location errors. Data were compiled from a variety of sources including planned tests, pre-deployment testing, opportunistic data collected from collars deployed in the field that became stationary after collar loss or animal mortality, and from collars tested during past research. Our methods were not intended to generate data suitable for side-by-side comparisons of accuracy among GPS collar models, but instead to present a representative range of location error from GPS collars, including those of three models from Televilt currently absent in the literature, for comparison with POSREC collars.

Field Deployment of POSREC Collars

We deployed POSREC 600-series store-on-board collars on mule deer (Krausman et al. 2004) beginning in March 2002 in Round Valley, California (37°25'N, 118°37'W), at the base of the Sierra Nevada, as part of long-term study of predator-prey interactions (Pierce et al. 2000, Pierce et al. 2004). Additional collars were similarly deployed on mule deer in the San Ysidro mountains, California (33°13'N, 116°30'W). Eleven collars were re-deployed during 2002–2005 when collars were recovered after animal mortality or after recapture and subsequent refurbishment of collars. Seven collars were re-deployed on bighorn sheep inhabiting the White Mountains (37°25'N, 118°14'W) and Sierra Nevada (36°32'N, 118°11'W) in 2004. Resultant field data included locations from a total of 50 animal deployments of 32 POSREC 600-series store-on-board GPS

collars. All collars were programmed by the manufacturer to attempt GPS fixes at intervals of 1–6 hours. We shipped collars to the former distributor, Telemetry Solutions (Walnut Creek, California) or, after 5 May 2005, directly to Televilt for download, and data were returned as e-mail attachments. We imported data into ArcView 3.3 (Environmental Systems Research Institute, Redlands, California) and used the Animal Movement extension² to connect sequential GPS positions. Data were projected into UTM coordinates and retained the WGS 1984 datum. We overlaid movement paths on a shaded relief map generated from a digital elevation model (DEM). Visual examination of locations was employed to identify suspect movements exhibiting an acutely angled out-and-back pattern (Fig. 1).

Fixed-Location Testing of GPS Collar Precision

Data from fixed locations were assembled from a combination of planned test sites, *ad-hoc* tests where drop-off mechanisms released collars from study animals or where animals died, and *ad hoc* locations of collars activated before deployment or after recovery. We used the mean of 3-D fixes from collars as the reference location (Dussault et al. 2001) and calculated error distance from this centroid. In the absence of an independent measure of the true location, this is a measure of precision rather than accuracy *per se*. We did, however, test for bias using the average of 100 3-D locations collected with a Rockwell PLGR (Rockwell Collins, Cedar Rapids, Iowa.), Garmin GPS12XL, or GPS III (Garmin, Inc., Lenexa, Kan.) receiver at each planned test location. Additional collar data were requested from Telemetry Solutions, at the time the distributor of Televilt products in the Americas.

We conducted tests of ATS 2000 model year ($n=8$) and Lotek GPS 2000 ($n=7$) collars in the vicinity of Seward, Alaska ($60^{\circ}06'N$, $149^{\circ}27'W$) from 6 May 2000, (4 days after selective availability was disabled; Lawler 2000) through 11 August 2000, at a total of 22 planned test sites and 2 dropped-collar sites. Most planned sites (78%) were located under closed-canopy (e.g., *Alnus crispa* or *Picea sitchensis*), as were 2 dropped collars. Locations were distributed over a range of slopes and aspects. Collars were oriented upright at approximately 0.5 m height; however, 30% of test collars were disturbed by black bears (*Ursus americanus*) during the 1–20 day trials, resulting in horizontal or downward orientation of the GPS antenna. We pooled the 953 (ATS) and 939 (Lotek GPS 2000) GPS positions by manufacturer. These data represent a range of worst-case conditions of canopy cover, topography, and collar orientation in a steeply sloped, high-latitude environment.

One POSREC collar was tested in an area of optimal sky view at 1-m height in sagebrush (*Artemesia tridentata*) habitat in Bishop, California ($37^{\circ}22'N$, $118^{\circ}24'W$) for 14 days. We augmented planned collar testing with retrospective analyses of instances where immobile GPS collars provided additional and unplanned data useful for determining the extent of location errors. Position data from fixed collars were obtained from POSREC collars that continued to acquire fixes while on deceased mule deer ($n=2$ collars) for 12 and 22 days prior to recovery. Data also were obtained from POSREC collars outside the homes of 2 biologists ($n=2$; 4 and 92 days), and from 3 collars active for 13–201 days on shelves inside a 1-floor wood-framed building in Bishop (hereafter “indoor” location), for a total of 663 positions collected under GPS receiving conditions ranging from optimal to marginal. Additional fixed-collar position data were collected

from Lotek 4400s ($n=2$; 2 and 12 days), Televilt Simplex ($n=3$; 6–119 days), and Televilt Tellus ($n=3$; 5–14 days) collars in 2003–2006 under similar conditions (Table 1). In an effort to replicate conditions at the indoor location where most fixed-location POSREC GPS collar data were collected, we activated 4 ATS model GPS2000 GPS collars for 16 days. We further employed a Garmin III Plus handheld GPS receiver to collect fixes over a 24-day period (median frequency of fixes=48.5 min) to explore the possibility that this indoor location could cause a marked increase in GPS location error.

Error Screening

We explored metrics to identify suspect out-and-back movements among GPS collar data from animal deployments and wrote scripts in ArcView to calculate angular deviation (Zar 1999), mean length and mean rate of sequential movement vectors (V_n, V_{n+1}), and the standard deviation of mean length and mean rate relative to prior and subsequent movement vectors. Movement vectors >500 m in length followed by vectors with azimuths of near 180 degree opposition were subjectively identified as “bad” when we judged the GPS fix improbable because of intervening topography, distance from other fixes, or unusually high speed of the implied movement. Movement vectors that appeared valid were subjectively identified as “good”. We used SPSS 11.0 for Mac OS X (SPSS Inc., Chicago, Illinois) to generate a logistic regression model of the probability that a GPS position was flawed as:

$$P_{bad} = \frac{e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}}{1 + e^{(\beta_0 + \beta_1 x_1 + \beta_2 x_2 + \dots + \beta_n x_n)}}$$

where P_{bad} is the probability that a movement represents an erroneous fix, β_0 is a constant and $\beta_1 \dots \beta_n$ are coefficients for predictor variables $x_1 \dots x_n$ (Hosmer and Lemeshow 2000).

Stepwise variable selection was employed with $P=0.15$ for entry and $P=0.20$ for

removal. We developed an ArcView 3.x extension incorporating the above calculations to generate a logistic probability for each position in an animal movement path.

RESULTS

Field Deployment of POSREC Collars

POSREC collar deployed on mule deer and bighorn sheep yielded a total of 89,283 positions, and produced star-shaped patterns when sequential fixes were connected (Fig. 1). Sequential vectors showed thousands of improbable out-and-back movements of up to 16 km (one-way), sometimes traversing 3,500 m mountains in winter, and returning to nearly the starting location ≤ 6 hours later. Elimination of 2-D fixes ($n=24,097$ or 27.0%) reduced the magnitude and frequency of suspect movements, but did not eliminate them (Fig. 1). These novel patterns were present in data from all POSREC collars ($n=32$) regardless of taxon or study area, though implausible fixes did not become apparent until sequential positions were connected. Once movement paths were generated, however, the star-shaped patterns were prominent and uncharacteristic of paths generated using other GPS collars (Fig. 2). POSREC collar data did not provide dilution of position (DOP) information that could have enabled the screening of fix quality (D'Eon and Delparte 2005). Neither did data include the number of satellites used to obtain a fix, though a fix category of “3-D+”, meaning that ≥ 5 satellites were used to solve for the position, is provided in addition to the conventional “2-D” and “3-D”³. These “3-D+” locations comprised 44.8% of GPS fixes from animal deployments, and displayed noticeably fewer anomalous fixes, though questionable locations remained (Fig. 5). A fourth category of “1-D” ($n=1,246$ or 1.4%) is what Televilt describes as a fix

calculated with <3 satellites, using parameters from previous positions³. We eliminated 1-D locations from our analyses.

Fixed-Location Testing of GPS Collar Precision

No GPS collar showed directional bias relative to averaged 3-D positions with a Rockwell PLGR, Garmin GPS12XL, or GPS III at planned test locations. The 95% confidence interval for each collar overlapped those of the averaged handheld GPS receiver.

POSREC collars displayed errors greater than any other collar over all categories except the 50th percentile for 3-D fixes (Table 1). Location errors for POSREC collars at the 95th percentile were in excess of 1 order of magnitude larger than for every other collar tested. These unique errors were characterized by a bimodal error distribution with the expected log-normal distribution for errors <100 m, and a second peak at approximately 600 m (Fig. 3). This unanticipated distribution persisted among 3-D fixes after elimination of 2-D positions. None of the 154 “3-D+” fixes, however, showed errors >135.8 m. The single POSREC collar tested under optimal sky-view conditions yielded results consistent with these unprecedented errors, with 3-D location errors $>1,000$ m and 2-D errors $>1,600$ m (Fig. 4). Further, tests with the handheld Garmin III receiver and with 4 ATS G2000 collars, at the indoor location where 3 POSREC collars collected 351 fixes, failed to produce errors of a magnitude approaching that of POSREC collars at the same location (Table 1).

Error Screening

We subjectively identified “good” ($n=1,322$) and “bad” ($n=1,358$) positions among data from POSREC collars deployed on mule deer and used 806 and 776,

respective, “good” and “bad” fixes to generate a logistic model. A random subset of 546 and 552 fixes were retained to test classification accuracy. Stepwise selection yielded a model including 3 predictors, in order of entry; AngDev, the angular deviation of sequential movement vectors (V_n, V_{n+1}), LengthN_NP1, the mean length of sequential movement vectors (V_n, V_{n+1}), and RateN_NP1, the mean rate of sequential movements (V_n, V_{n+1}). Examination of variable RateN_NP1 showed that some collars were strongly influenced by variation in the time between successful GPS fixes, due to programming of uneven fix intervals, or consecutive failures of scheduled GPS fixes. To avoid overfitting and ensure broad applicability among collar programs, taxa, and study areas we chose the 2-predictor model:

$$P_{bad} = (-4.77487 + 0.002656 * \text{LengthN_NP1} + 0.02860 * \text{AngDev})$$

A classification test at 50% probability yielded 100% concordance with 552 subjectively identified “bad” fixes and 99.1% concordance identifying 541 fixes as “good,” while incorrectly classifying 5 as “bad.” Application of the logistic model to 89,232 movement lines generated from all ≥ 2 -D fixes at the 50% probability level resulted in classification of 31,672 (36.0%) fixes as bad. Of these, 18,028 were 2-D, 6,407 “3-D,” and 7,237 “3-D+.” Screening with this approach greatly reduced the frequency of anomalous movements (Fig. 6).

DISCUSSION

Field deployment of POSREC collars generated movement patterns unlike those from any other GPS collar we have examined (e.g., Fig. 2) and showed numerous movements that were obviously improbable although inapparent when viewed solely as a swarm of points (Fig. 1). Location errors obtained from POSREC collars exceeded those of any GPS collar in our testing or reported in the literature. Evaluation of the precision of ATS, Lotek, and Televilt Simplex and Tellus collars produced location errors consistent with those reported for various conditions of terrain, canopy, and collar orientation using ATS, Lotek, and Telonics collars (D'Eon 2003, Di Orio et al. 2003, Cain et al. 2005, D'Eon and Delparte 2005).

In our effort to quantify the errors we suspected after recovering POSREC collars used in 50 animal deployments, we sought and received 191 positions from a POSREC collar (serial no. C600-176), which had been activated at an outdoor location before shipping to a customer (Q. Kermeen, Telemetry Solutions, personal communication). The maximum location error from this POSREC collar was 118.4 m (Table 1, identified as “prototype”), and characteristic of a non-defective GPS unit, but in sharp contrast to location errors we obtained from 8 POSREC collars, including units with serial numbers bracketing C600-176. For example, collar C600-175, used in our optimal sky-view test, showed errors >500 m in 20.7% of 101 fixes (Fig. 4), and collar C600-219 demonstrated errors of >1,000 m in 26.6% of 45 fixes (all 2-D) at the indoor location. Data provided from collar C600-176 had been collected at 30-minute intervals, while we present data for ≥ 1 hour intervals, but (Cain et al. 2005) reported no difference in location accuracy within this range of fix intervals. Personnel at Telemetry Solutions could not explain the

difference and referred us to Televilt. We sent Televilt a summary of our data and requested the source of the unprecedented errors in every collar tested and an explanation for the normal performance of collar C600-176. Weeks later, after repeatedly requesting an explanation, we received the response, “To make it short: It is the performance of the GPS receiver that is the problem” (Anders Lindgren, Televilt/TVP Positioning AB, personal communication). We were further informed that the problem was with, “the SiRFStarI receivers, that we used in your collars,” that have “a larger spread of data,” and that collar C600-176, “most likely has a SiRFStarII GPS receiver,” and was, “one of our prototypes.” Mr. Lindgren asserted that after February 2003, collars with serial numbers >425 used the newer GPS receiver. No remedy was offered for the 32 defective collars. If the statement about the serial numbers is accurate, some 425 POSREC-Science™ 600 collars containing the problematic GPS receiver have been sold, and can be expected to also show extraordinarily large location errors. The problem is not isolated to the 600-series collars we purchased. We were referred to a user of POSREC-Science™ 300 collars who had documented the flaw, and were also informed that over 1,000 POSRECcollars were sold in the Americas (Q. Kermeen, personal communication).

In the absence of a solution from the manufacturer, researchers are faced with a dilemma of how to salvage flawed POSREC data. Frequent location errors of several kilometers render data unacceptable for all but the most course-scaled evaluation of habitat selection or migration, thereby necessitating some type of data screening. Screening to retain only "3-D" or "3-D+" fixes magnifies inherent bias against locations where canopy cover, topography, or collar orientation preclude acquisition of high-quality fixes (Frair et al. 2004, D'Eon and Delparte 2005). While our data indicate that

"3-D+" fixes have a lower frequency of errors; screening for "3-D+" fixes would remove >55% of successful fixes, yet still retain suspect locations (Fig. 5).

We created the "BadFix" extension for ArcView 3.x, which evaluates the length and angular deviation of movement vectors in a logistic regression model. Application of BadFix reduces habitat-associated biases by screening positions regardless of fix quality. A limitation of the screening approach we employ in BadFix is the identification of some authentic movements that approximate an out-and-back pattern. When we used the BadFix extension to screen movements of a Lotek GPS4400s collar deployed on a male puma (*Felis concolor*), 16 of 743 (2.2%) movements were flagged as "bad" at the 95% probability level, although we had no reason to believe GPS error was involved. Instead, the return of the puma to feed at a kill site approximated the out-and-back pattern the BadFix extension was designed to identify. When movements of a male bighorn sheep wearing a Televilt Telus GPS collar were screened at 95% probability, only 25 of 5150 (0.5%) of movements were identified as "bad". In both instances, a smaller sample of suspect locations were identified for further evaluation by the researcher. We believe that the screening method we present should be considered for its effectiveness at identifying potentially erroneous locations, while including more unaffected data and remaining less influenced by habitat-associated bias when compared to screening by fix quality alone.

Management Implications

We reiterate the recommendations of D'Eon et al. (2002) that researchers screen raw GPS data for anomalous positions that are clearly impossible, regardless of what model GPS collar is employed. Although an individual position may seem plausible, when it is immediately preceded and followed by near-parallel movements of unusually

long distance over short times, the reliability of the fix should be questioned. Thus, we add the suggestion that a tool such as Animal Movement (Hooge and Eichenlaub 1997) be employed to aid in visual identification of anomalous fixes. We further recommend employing an automated screening tool such as the BadFix extension for larger data sets or when errors are common. We employed BadFix not only for triage of POSREC data, but for screening movement data from collars that now collect >10,000 locations and for identifying errors introduced by remote data transmission over UHF and VHF.

Researchers employing remote data download via direct radio may find automated screening useful for flagging artifacts of transmission we have experienced using VHF and UHF systems. The BadFix extension for ArcView 3.x is available for download from the World Wide Web at (<http://arcscrips.esri.com/details.asp?dbid=14434>) and is provided as open-source and may be freely modified.

We echo the recommendations of (Moen et al. 1997, Rempel and Rodgers 1997) that researchers understand factors affecting the type and precision of GPS locations, and further suggest that sample data be obtained from the model of collar being considered. Although our request for sample data was met with the provision of data from a prototype collar that was not the same as the product we purchased, requests of other manufacturers may be handled in a forthright manner. We further recommend that GPS collar users test and evaluate results of their collars before deployment. This recommendation is only practicable for collars that allow data retrieval by the user, unlike the POSREC model.

ACKNOWLEDGMENTS.

This study was supported by the California Department of Fish and Game (CDFG) Deer Herd Management Improvement Program, the CDFG Sierra Nevada

Bighorn Sheep Recovery Program, the California Deer Association, and the Department of Biological Sciences at Idaho State University. We thank I. Oshima for suggestions on improving ArcView scripts, M. C. Nicholson for his original GIS work that contributed to the BadFix extension, and A. Ellsworth for the loan of collars. This is a contribution from the Sierra Nevada Bighorn Sheep Recovery Program, and is Professional Paper 052 from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- Cain, J. W., P. R. Krausman, B. D. Jansen, and J. R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin* 33:926-934.
- D'Eon, R. G., R. Serrouya, G. Smith, and C. O. Kochanny. 2002. GPS radiotelemetry error and bias in mountainous terrain. *Wildlife Society Bulletin* 30:430-439.
- D'Eon, R. G. 2003. Effects of a Stationary GPS Fix-rate Bias on Habitat-selection Analyses. *The Journal of Wildlife Management* 67:858-863.
- D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *The Journal of Applied Ecology* 42:383-388.
- DeCesare, N. J., J. R. Squires, and J. Kolbe. 2005. Effect of forest canopy on GPS-based movement data. *Wildlife Society Bulletin* 33:935-941.
- Di Orio, A. P., R. Callas, and R. J. Schaefer. 2003. Performance of two GPS telemetry collars under different habitat conditions. *Wildlife Society Bulletin* 31:372-379.

- Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot. 1999. Evaluation of GPS telemetry collar performance for habitat studies in the boreal forest. *Wildlife Society Bulletin* 27:965-972.
- Dussault, C., R. Courtois, J.-P. Ouellet, and J. Huot. 2001. Influence of satellite geometry and differential correction on GPS location accuracy. *Wildlife Society Bulletin* 29:171-179.
- Frair, J. L., S. E. Nielsen, and E. H. Merrill. 2004. Removing GPS collar bias in habitat selection studies. *The Journal of Applied Ecology* 41:201-212.
- Gau, R. J., R. Mulders, L. M. Ciarniello, D. C. Heard, C. L. B. Chetkiewicz, M. Boyce, R. Munro, G. Stenhouse, B. Chruszcz, M. L. Gibeau, B. Milakovic, and K. L. Parker. 2004. Uncontrolled field performance of Televilt GPS-Simplex™ collars on grizzly bears in western and northern Canada. *Wildlife Society Bulletin* 32:693–701.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied Logistic Regression*. Second edition. John Wiley & Sons, New York, New York, USA.
- Krausman, P. R., V. C. Bleich, J. W. Cain, T. R. Stephenson, D. W. DeYoung, P. W. McGrath, P. K. Swift, B. M. Pierce, and B. D. Jansen. 2004. Neck lesions in ungulates from collars incorporating satellite technology. *Wildlife Society Bulletin* 32:987-991.
- Lawler, A. 2000. Scientists gain access to sharper GPS signal. *Science* 288:783.
- Moen, R., J. Pastor, and Y. Cohen. 1996. Effects of moose movement and habitat use on GPS collar performance. *The Journal of Wildlife Management* 60:659-668.

- Moen, R., J. Pastor, and Y. Cohen. 1997. Accuracy of GPS telemetry collar locations with differential correction. *Journal of Wildlife Management* 61:530-539.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology* 81:1533-1543.
- Pierce, B. M., R. T. Bowyer, and V. C. Bleich. 2004. Habitat Selection by Mule Deer: Forage Benefits or Risk of Predation? *The Journal of Wildlife Management* 68:533-541.
- Rempel, R. S., and A. R. Rodgers. 1997. Effects of differential correction on accuracy of a GPS animal location system. *The Journal of Wildlife Management* 61:525-530.
- Rempel, R. S., A. R. Rodgers, and K. F. Abraham. 1995. Performance of a GPS animal location system under boreal forest canopy. *The Journal of Wildlife Management* 59:543-551.
- Zar, J. H. 1999. *Biostatistical analysis*. Fourth edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

FOOTNOTES

¹ Present address: California Department of Fish and Game, P.O. Box 3222, Big Bear City, CA 92314

² Hooge, P. N., and B. Eichenlaub. 1997. Animal movement extension to ArcView. Version 1.1. Alaska Biological Science Center, U.S. Geological Survey, Anchorage, Alaska, USA.

³ Televilt/TVP Positioning AB, unpublished document, "What is fix type.txt"

Table 1. Percentile^a location errors (m) for 8 GPS collar models and 1 handheld GPS unit with exceptional errors denoted by bold type.

GPS Model	Location	All 2-D and 3-D fixes					3-D fixes					
		<i>n</i>	50%	95%	99%	100%	<i>n</i>	50%	95%	99%	100%	
ATS	Year 2000	Outdoor ^b	953	9.3	65.5	161.7	486.3	660	8.3	42.8	107.9	486.3
	G2000	Indoor ^c	66	10.5	82.2	___	167.3	28	7.8	33.4	___	37.2
Garmin	III Plus	Indoor ^c	100	8.0	39.0	171.5	172.7	82	7.4	36.1	___	55.5
Lotek	GPS2000	Outdoor ^b	939	11.1	64.4	240.8	338.4	388	10.1	41.1	240.7	338.4
	GPS4400s	Outdoor ^d	98	5.5	24.0	___	117.2	94	5.5	20.0	___	72.7
Televilt	Posrec	Both ^e	663	200.7	1399.9	2213.6	3352.9	332	8.1	467.3	1211.0	1486.3
	Simplex	Both ^f	1117	8.3	36.0	73.6	317.4	378	7.8	18.9	28.2	34.1
	Tellus	Both ^g	289	14.7	71.5	174.0	465.6	271	14.0	71.2	191.3	465.6
	Prototype ^h	Outdoor	191	6.9	21.0	50.2	118.4	147	6.5	17.4	82.8	118.4

^a Percentile errors are also referred to as CEP (circular error probable).

^b Planned test locations (ATS, Lotek) and unplanned tests at dropped collar locations ($n=385$ of 939 fixes; Lotek), vicinity of Seward, Alaska.

^c Planned test location inside wood-framed building, Bishop, CA.

^d Pre-deployment tests on truck dashboard, Bishop, CA.

^e Planned test in optimal sky view area ($n=101$ fixes), unplanned tests at deer mortality locations ($n=120$ fixes), unplanned tests outside the homes of biologists ($n=91$ fixes), and unplanned test location inside a wood-framed building ($n=351$ fixes), vicinities Bishop and San Ysidro, CA.

^f Pre-deployment test in windowsill ($n=758$ fixes) and truck dashboard ($n=146$ fixes), and unplanned test at dropped collar locations ($n=213$ fixes), vicinity Bishop, CA.

^g Pre-deployment test in windowsill ($n=81$ fixes) and truck dashboard ($n=15$ fixes), unplanned tests at bighorn sheep mortality location ($n=193$ fixes), vicinity Bishop, CA.

^h Data from POSREC prototype collar (see discussion).

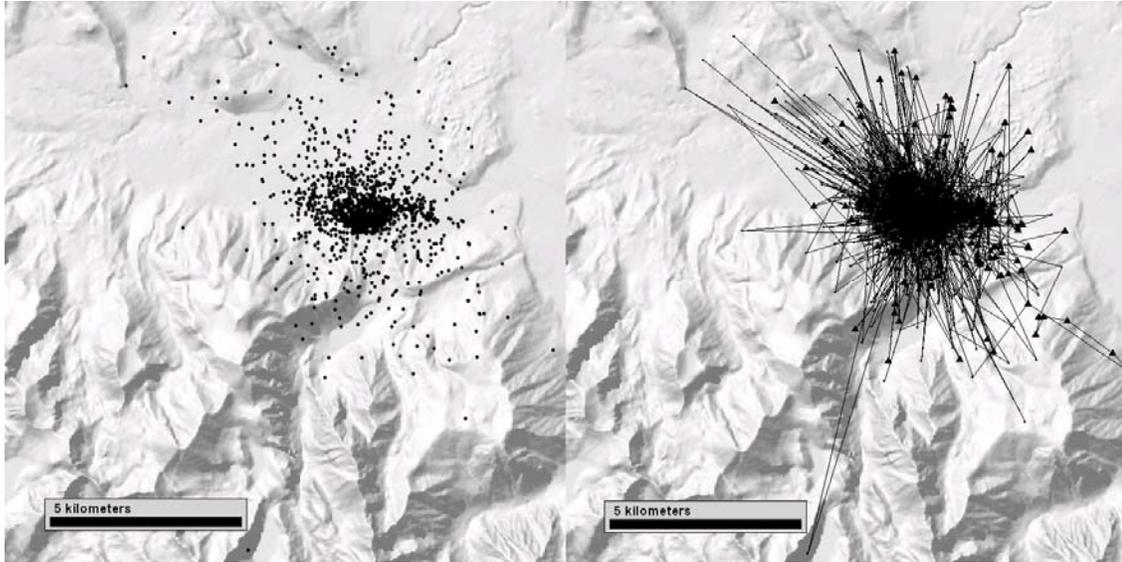


Figure 1. All point locations (left) and movement path (right) generated from POSREC GPS collar deployed on mule deer RVD210, 10 Apr 2002–21 Sep 2002; all fixes (2-D and 3-D; $n=1895$). "3-D" and "3-D+" fixes ($n=1344$) denoted by triangles.

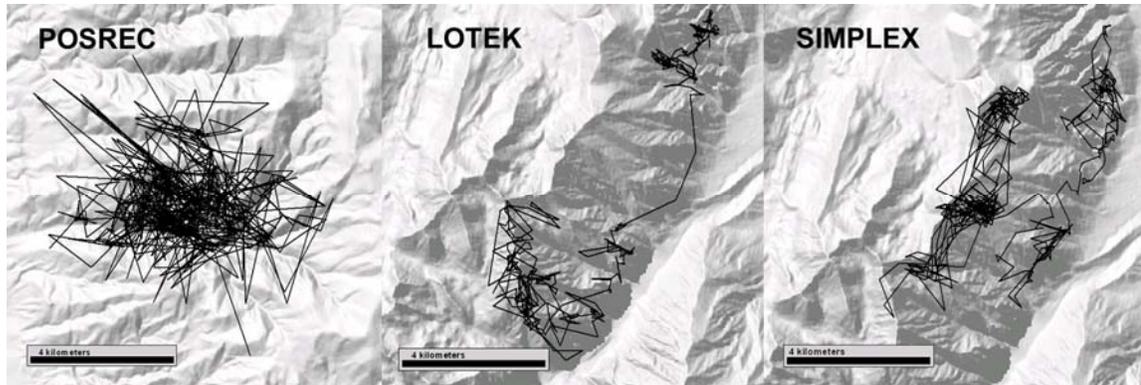


Figure 2. GPS collars deployed on a desert bighorn ewe D7 (POSREC; n=852 locations) and Sierra Nevada bighorn ewe S62 (Lotek GPS 4400s; n=1035 locations) and ram S18 (Televilt Simplex; n=651 locations) over the same period: 20 Mar–8 Sep in 2004 (Posrec, Simplex) and 2005 (Lotek). All fixes (2-D and 3-D) are included.

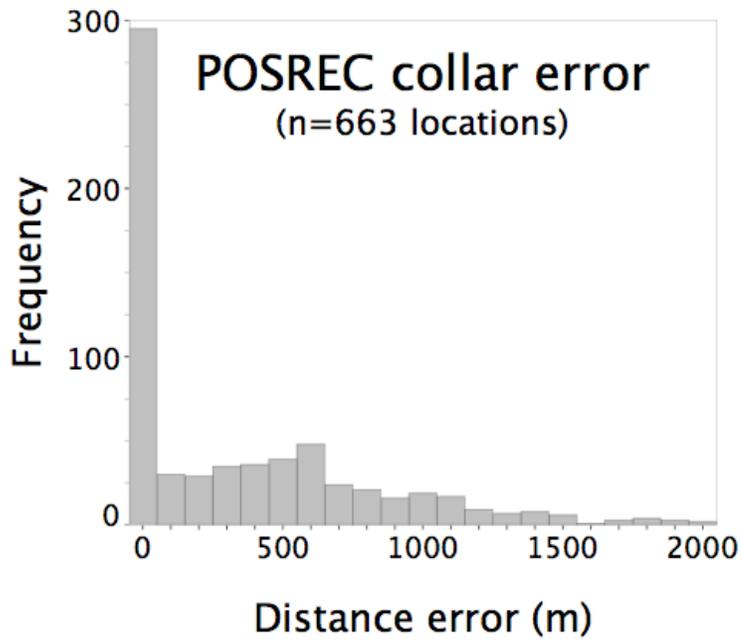


Figure 3. Error distribution (all 2-D and 3-D fixes) from fixed-location POSREC collars.

Errors >2100 m (n=7) not illustrated.

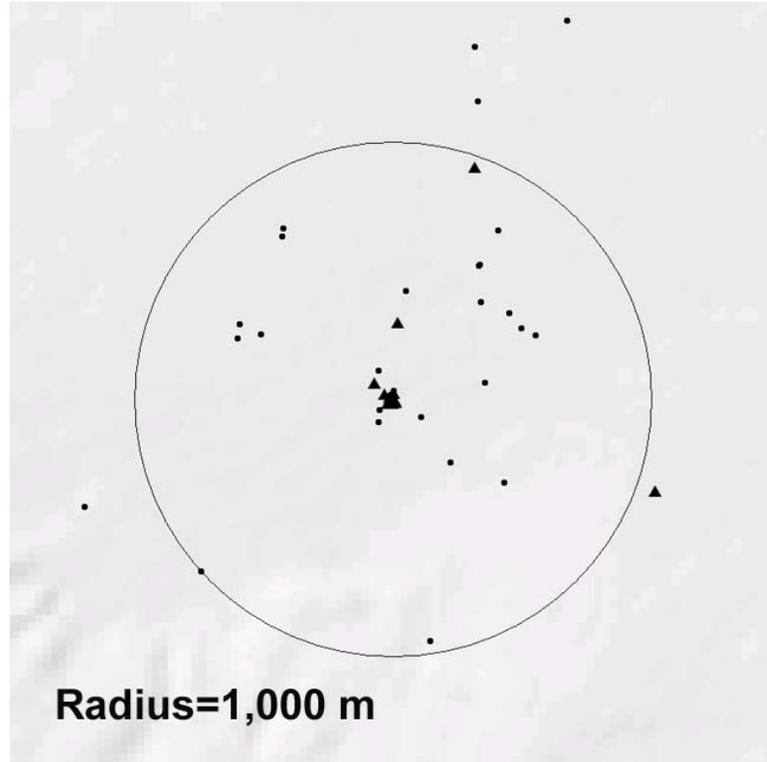


Figure 4. POSREC collar C600-175 tested under optimal sky visibility. N=101 fixes (2-D and 3-D). 3-D fixes (n=76) denoted by triangles.

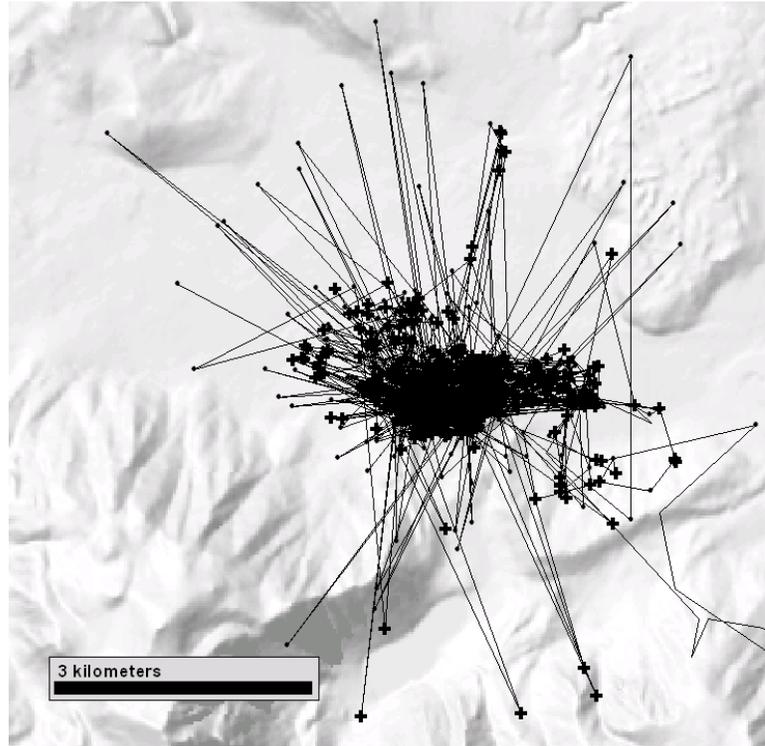


Figure 5. POSREC GPS collar movement path, mule deer RVD210, 10 Apr 2002–21 Sep 2002, generated from 3-D and better fixes (n=1344). Crosses denote "3-D+" fixes (n=840).



Figure 6. POSREC GPS collar movement path, mule deer RVD210, 10 Apr 2002–21 Sep 2002, generated after screening all ≥ 2 -D fixes using the BadFix ArcView extension at the 50% probability level (n=1,064 fixes remaining).

Chapter III.

Resource selection by an endangered ungulate: a multiscale test of predator-induced range abandonment

Abstract. We investigated influences of risk of predation by mountain lions (*Puma concolor*), topographic metrics at multiple scales, and vegetation, land, and snow cover, on resource selection by Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), an endangered taxon, during winters 2002–2007, in the Sierra Nevada, California, USA. We hypothesized that those mountain ungulates would trade off rewards accrued from using critical low-elevation habitat in winter for the safety of areas with reduced risk of predation. We also compared the tradeoff between forage and risk of predation in years of drought versus wet years. We tested the prediction that differences in quality of forage at low-elevations versus high-elevations were less in years of below-average precipitation than in wet years, yielding a reduced benefit of migration to low-elevations during drought, compared with years of above-average precipitation. Sierra Nevada bighorn sheep did not trade off benefits of forage for reduced risk of predation, but selected areas of high solar radiation, where risk of predation by mountain lions was greatest, while mitigating indirect risk of predation by selecting for steep, rugged terrain. Bighorn sheep selected more strongly for areas where mountain lions were active, than for low-elevation habitat in winter, likely because mountain lions were most active in those areas of bighorn winter ranges overlapping ranges of mule deer (*Odocoileus hemionus*), where both ungulates accrued forage benefits. We demonstrated reduced benefit of migration to low elevation during drought years, when the difference in quality of forage was

significantly less than in years of above-average precipitation, providing an alternative explanation to the predator-induced abandonment hypothesis for the disuse of low-elevation winter range observed during drought years.

Key words: *Ovis canadensis sierrae*, *Puma concolor*, predation risk, resource selection, remote sensing, Sierra Nevada, NDSI, NDVI.

Introduction

Ungulates face decisions concerning habitat selection and foraging behavior that are shaped by adaptations for enhancing foraging efficiency (MacArthur and Pianka 1966), while simultaneously reducing risk of predation (Bleich 1999, Kie 1999). Those animals living in temperate or arctic environments, where a seasonal abundance of forage coincides with increased nutrient demands of late gestation and lactation (Barboza and Bowyer 2000, Barboza and Bowyer 2001, Barboza et al. 2009), must balance the need to acquire nutrients against constraints from risk of predation (Berger 1991, Bowyer et al. 1998, Barten et al. 2001). Many populations of ungulates migrate between discrete seasonal ranges (McNaughton 1985, Fryxell et al. 1988, Nicholson et al. 1997, Rachlow and Bowyer 1998, Monteith et al. 2011, Lendrum et al. 2012, 2013), with those occupying montane environments obtaining high-quality resources by selecting among elevations that enable exploitation of new growth in forage (Hebblewhite et al. 2008, Monteith et al. 2011). Benefits of migration to areas of high-quality forage must outweigh increased risk of predation to comprise an evolutionarily stable strategy (ESS; Maynard Smith and Price 1973). The optimal solution between energy maximization and risk minimization (Belovsky 1984, Pyke 1984) differs among life-history stages (Bowyer 2004), and is dynamic where resources and risk vary over space and time (Bowyer and

Kie 2006). Evaluation of habitat selection under risk of predation must account for differences between the sexes in risk tolerance and foraging strategy (Bleich et al. 1997, Bowyer 2004, Schroeder et al. 2010, Oehlers et al. 2011).

Predator avoidance operates through both indirect mechanisms that affect the likelihood of encountering, detecting, or eluding a predator, and direct means that minimize the odds of success of a predator in capturing prey upon detection (Kruuk 1972, Bleich 1999). Mechanisms of direct predator avoidance include sight (Berger 1978, Risenhoover and Bailey 1980), as well as olfactory and auditory cues (Kotler and Holt 1989, Brown et al. 1999, Berger et al. 2001). In the absence of overt signs of a predator, mountain sheep (*Ovis* spp.) may assess the likelihood of encountering and escaping a predator as a function of habitat (Berger 1991, Rachlow and Bowyer 1998, Schroeder et al. 2010). Visually unobstructed habitats enable ocular detection of predators (Risenhoover and Bailey 1980, Frid 1997, Rachlow and Bowyer 1998), whereas formation of groups can reduce the level of vigilance required of individuals and dilute the odds of an individual being selected as prey (Hamilton 1971, Berger 1978, Bertram 1978, Lima and Dill 1990, Molvar and Bowyer 1994, Kie 1999). Proximity to a refuge (e.g., steep and rugged escape terrain; McCann 1956, Geist 1971) may confer protection from some predators, in part, because coursing predators seldom use those areas (e.g., coyotes, *Canis latrans*; Bleich et al. 1997; gray wolves, *C. lupus*; Barten et al. 2001, Farmer et al. 2006).

Mountain sheep occupy montane and desert environments and some populations migrate between high-elevation summer ranges and lower-elevation winter ranges, corresponding to the progression of new growth in grasses, forbs, and shrubs (Geist 1971,

Wehausen 1980, Festa-Bianchet 1988). Variation in temperature, precipitation, and vegetation phenology may alter maternal behavior and habitat selection by mountain sheep (Rachlow and Bowyer 1994, 1998, Whiting et al. 2010). Selection of resources is subject to constraints imposed by perceived risk; sub-lethal effects of risk of predation may have profound influences on behavior and habitat selection (Lima 1998, Creel and Christianson 2008), and incur physiological costs (Creel et al. 2007). Middleton et al. (2013), however, determined there was no association between sub-lethal response to risk of predation by wolves on pregnancy or body condition in North American elk (*Cervus elaphus*). Responses to fear of predation have been posited to drive shifts in habitat selection, ultimately resulting in negative demographic effects among large herbivores (Wehausen 1996, Ripple et al. 2001).

Mountain lions (*Puma concolor*) are the primary predators of mountain sheep in areas of sympatry, and have been implicated as a threat to populations of Sierra Nevada bighorn sheep (Sierra Nevada Bighorn Sheep; *O. c. sierrae*; Wehausen 1996), an endangered taxon (U.S. Fish and Wildlife Service 2008). These large felids may cause substantial mortality in some populations of mountain sheep (Ross et al. 1997, Hayes et al. 2000, Schaeffer et al. 2000, Rominger 2004, Festa-Bianchet et al. 2006), but questions remain about the potential for sub-lethal effects as a consequence of changes in behavior or habitat selection by bighorn sheep. A precipitous decline in the largest population of Sierra Nevada bighorn sheep at Mount Baxter, California, USA, from 1987 to 1991, was attributed to decreased recruitment after females failed to occupy high-quality, low-elevation winter ranges in response to risk of predation by mountain lions (Wehausen 1996). Wehausen (1996) concluded that “range abandonment” by Sierra Nevada bighorn

sheep was a response to perceived risk of predation, and not to effects of drought on forage, or to removal of large numbers bighorn sheep from the winter range for translocation. Although low-elevation helicopter flights were shown to cause temporary movements of bighorn sheep (Bleich et al. 1990a, 1994), cumulative effects of repeated low-level flights, such as those employed in helicopter capture and removal of 103 bighorn sheep (Bleich et al. 1990b), are unknown.

The effect of 6 years of drought (Roos 1992, Pierce et al. 2012), coincident with the decline in Sierra Nevada bighorn populations, remains uninvestigated, and offers an alternative explanation for declines in those populations of bighorn sheep. Previous studies caution that removals may cause negative demographic consequences (Stevens and Goodson 1993), yet such alternative factors for declines in Sierra Nevada bighorn sheep have not been adequately investigated (Villepique et al. 2011).

Evaluation of alternatives to predator-induced range abandonment (Wehausen 1996) is limited by the absence of information from telemetered animals, and by lack of information on forage or snow conditions, which likely played a principal role in habitat selection by bighorn sheep in winter. The availability of archived, remotely sensed data, however, enable retrospective evaluation of indices of snow cover and forage condition from the period of reported range abandonment during winter.

Variation in forage quality and quantity can be indexed remotely with Normalized Difference Vegetation Index (NDVI), calculated from multispectral satellite imagery, at spatial and temporal resolutions dictated by the satellite platform employed (Pettorelli et al. 2005). Large- (64-km pixel) and intermediate-scale (1-km pixel) imagery were correlated with vegetation phenology (Pettorelli et al. 2005, 2007). Peak values of NDVI

also were correlated with values of fecal crude protein (Hamel et al. 2009), an index of dietary quality (Leslie et al. 2008), thereby validating NDVI as a useful index to quality of forage used by ungulates. Further, values of NDVI were correlated with timing of migration in ungulates from imagery on scales of 1 km (Monteith et al. 2011), and 250 m (Hebblewhite et al. 2008), as well as with fine-scale models of resource selection (30-m pixel; Hansen et al. 2009).

Remote sensing of NDVI may be applied to a single point in time to index spatial variation in vegetation quality and quantity (Hansen et al. 2009), with NDVI as a proxy for photosynthetic activity and vegetation cover. Alternatively, the timing of phenomena, such as migration or peak dietary quality, may be identified with spatial and temporal composites or indices generated from a number of sequential images (Hebblewhite et al. 2008, Hamel et al. 2009, Monteith et al. 2011). Rarely are temporal and spatial variation investigated simultaneously, because of scalar limits on one of those dimensions (Beck et al. 2008).

For sub-lethal effects of predation risk to result in the severe demographic consequences posited by Wehausen (1996), bighorn sheep must have made disproportionate tradeoffs by giving up nutrients in exchange for reduced risk of predation. Under that hypothesis, a landscape-scale shift in habitat selection must have occurred, wherein Sierra Nevada bighorn sheep avoided traditional low-elevation winter ranges in response to risk of predation from mountain lions. If bighorn sheep trade off risk through use of high-elevation habitat, we expected bighorn sheep that were subject to substantial risk of predation to select areas of lesser risk, but with lower-quality forage, and concomitantly reduced nutrient availability, in both wet and dry years (Table 1).

Alternatively, if landscape-scale movements are not evident, we expected bighorn sheep to remain in areas with high predation risk to access quality forage, while exhibiting antipredator behaviors through fine-scale selection of rugged and steep terrain (Table 1).

Study Area

The eastern slope of the Sierra Nevada range is a rugged escarpment rising from the Owens Valley, forming the western boundary of the Great Basin in eastern California, USA. The highest peaks and steepest slopes are located in the southern portion of the range in Inyo and Mono counties, California (centroid 37°11'N, 118°23'W), where four distinct populations of Sierra Nevada bighorn sheep occupied rugged granitic slopes (Mono Basin, Wheeler Ridge, Mount Baxter, and Mount Langley; Schroeder et al. 2010; Fig. 1). We focused on the two largest populations of Sierra Nevada bighorn sheep: Wheeler Ridge and Mount Baxter. Elevations of winter ranges were 1,500–4,100 m at Wheeler Ridge, and 1,300–4,100 m at Mount Baxter. Winter ranges of both populations of bighorn sheep overlapped winter ranges of migratory herds of mule deer (*Odocoileus hemionus*; Johnson et al. 2013, Monteith et al. 2014). The predominant vegetation community at low elevation was Great Basin sagebrush steppe, dominated by sagebrush (*Artemisia tridentata*) and antelope bitterbrush (*Purshia tridentata*; Storer and Usinger 1968), whereas mountain whitethorn (*Ceanothus cordulatus*), mountain mahogany (*Cercocarpus ledifolius*), and horsebrush (*Tetradymia canescens*) were common at middle elevations. Trees, including Jeffrey pine (*Pinus jeffreyi*), and juniper (*Juniperus occidentalis*) were sparsely distributed throughout middle elevations, with grasses (*Achnatherum speciosa*, *Festuca* spp.), and buckwheat (*Eriogonum* spp.) common as understory species. At high elevations (3,300–4,300 m), characteristic alpine vegetation

included alpine crested wheatgrass (*Agropyron* spp.), sedges (*Carex* spp.), and vetches (*Astragalus* spp.; Schroeder 2010).

Methods

Animal capture

Bighorn sheep.—During 2002–2007, we captured bighorn sheep with a net gun fired from a helicopter (Krausman et al. 1985). Bighorn sheep were physically restrained and transported to a central processing area where samples were collected and a GPS (global positioning system) collar (described later) and a small secondary collar containing a VHF (very high frequency) transmitter were fitted to adult (>1 year old) bighorn sheep.

Mountain lions.—We captured mountain lions from 2002 to 2009 by pursuit with hounds, employing techniques described by Pierce et al. (1998, 2000) or by opportunistic darting. Adult mountain lions were immobilized with Telazol (4.4 mg/kg; Pierce et al. 2000), with an extra-long-range projector (Palmer Cap-Chur, Inc., Powder Springs, Georgia, USA). When proximity to water presented a potential risk of drowning, we used darts equipped with a VHF transmitter (Pneudart Inc., Williamsport, Pennsylvania, USA; Kilpatrick et al. 1996) to facilitate rapid location of mountain lions after immobilization. Mountain lions were fitted with GPS collars (described later) prior to release. Capture methods for bighorn sheep and mountain lions followed guidelines of the American Society of Mammalogists (Sikes et al. 2011), and were approved by the Institutional Animal Care and Use Committee (protocol #: 0202) at the University of Alaska Fairbanks.

Spatial analyses

Bighorn sheep.—Four models of GPS collars were deployed on bighorn sheep: Advanced Telemetry Systems GPS 2100 ($n = 6$; Isanti, Minnesota, USA), Lotek Wireless 4400s ($n = 2$; Newmarket, Ontario, Canada), and Televilt Simplex ($n = 16$), and Televilt Telus ($n = 4$; TVP Positioning AB, Lindesberg, Sweden). Collars were programmed with heterogeneous schedules of 3–720 GPS locations/day. Data from GPS collars were censored for 2 days post-capture to decrease the influence of atypical movements immediately following capture (Quinn et al. 2012); erroneous GPS locations were eliminated by screening in ArcView 3.2 (Environmental Systems Research Institute, Redlands, California, USA; ESRI) with the BadFix extension (Villepique et al. 2008). We analyzed data for animals with ≥ 10 days of location data in winter (January–April).

We used Home Range Tools for ArcGIS (Rodgers et al. 2007) and ArcGIS 9.2 software (ESRI, Redlands, California, USA) coupled with data from GPS collars rarified to one randomly selected location per animal per week to define the study areas as the composite home ranges for all bighorn sheep in winter with a 95% adaptive-kernel and smoothing factor of 80% h_{ref} (Kie 2013; Fig. 1).

Analysis of resource selection used only high-quality locations, after elimination of 2-D locations and those locations where dilution of precision (DOP) was ≥ 10 (D'Eon and Delparte 2005, Frair et al. 2010). Such screening introduced biases against detecting use of areas with high canopy closure or areas where available sky is obscured by topography (Frair et al. 2004, 2010, Cain et al. 2005). Closed canopy was rare in our study area and, where present, generally was avoided by mountain sheep (Geist 1971). Cain et al. (2005) demonstrated a reduction in 3-D fixes of 36% in areas with $< 33\%$

available sky versus those locations with >66% available sky. We acknowledge a likely bias against detection of use in areas where close proximity to steep escape terrain limited available sky necessary for satellite fixes. High-quality GPS data were rarified by selecting the location nearest in time to solar noon. We tested for independence of locations using the program ASSOC1 (Weber et al. 2001), assuming that animals with a proximity of <200 m for >25% of locations represented animals in the same group.

We calculated mean GPS location error, based on published error estimates (D'Eon and Delparte 2005, Villepique et al. 2008), and weighted by the proportion of GPS locations from each model of collar in our analysis, to assess appropriate scale for evaluation of third-order habitat selection (Johnson 1980, Montgomery et al. 2011). Location error of 3-D fixes, from previous studies, averaged 6.3 m (i.e., 50% circular error probable; CEP) and 95% CEP = 28.6 m. Ensuring that the accuracy of locations of animals is comparable to the scale of habitat maps is a key consideration when evaluating resource selection (Montgomery et al 2011). Our estimates of GPS location error were comparable in scale to geometric accuracy of level 1T TM data (approximately ≤ 30 m, or 1 pixel; http://landsathandbook.gsfc.nasa.gov/pdfs/Landsat7_Handbook.pdf).

Available locations.—Ten locations were randomly assigned within a 2.4-km radius of the location for each bighorn sheep (Fig. 2) with Hawth's Analysis Tools 2.10 for ArcGIS 9.2 (Beyer 2004). The 2.4-km radius reflected availability of temporally varying resources within a distance an animal could readily move in 24 h at the rate of 100 m/h noted for 16.3% of movements during 1–36 h intervals (Fig. 3; Arthur et al. 1996). Available locations were further constrained by the 95% composite home range for bighorn sheep; random points falling outside that composite home range for the

population were eliminated and new random points cast to achieve 10 available matched-case locations for each animal location (Boyce 2006).

Locations of mountain lions.—We deployed four models of GPS collars on mountain lions: Lotek Wireless 4400s ($n = 9$), Televilt Simplex ($n = 23$), Televilt Telus ($n = 3$), and Northstar RASSL Tracker ($n = 4$; Northstar Science and Technology, King George, Virginia, USA). Collars were programmed to collect 6–10 GPS locations per day; 1–3 locations during mid-day (10:00–14:00), and 5–7 locations during crepuscular and nighttime hours (18:00–06:00). Risk of predation by mountain lions was indexed by two measures: the distribution of locations of GPS collars from mountain lions active (and likely hunting) within winter range of bighorn sheep; and the distribution of locations where bighorn sheep were killed or cached by mountain lions.

We defined locations of “active” mountain lions by selecting locations of GPS collars not associated with cached prey or resting places (Knopff 2010). Clusters of locations characteristic of cached prey or of resting sites, where mountain lions were not actively hunting, were selected with a C++ program (Supplement 1; cluster.c), which identified clusters of locations based on temporal and spatial parameters. We set the spatial tolerance to <200 m within ≤ 6 days (Knopff et al. 2009). We retained only one GPS location for each cluster, to avoid pseudoreplication of locations where inactive mountain lions were likely resting (Knopff 2010), or feeding at a kill (Pierce et al. 1998) and thus not actively hunting. We retained all GPS locations (i.e., 2-D and 3-D locations of all DOP values) to increase the sample of locations of active mountain lions for calculation of utilization distributions (i.e., second order selection; Johnson 1980).

Locations where bighorn sheep were cached by mountain lions ($n = 39$) were identified by evaluating clusters of locations from GPS collars deployed on mountain lions ($n = 10$; Knopff et al. 2009), investigating mortality signals from collared bighorn sheep ($n = 13$), or from kills encountered while following lion tracks or trailing hounds that located a carcass ($n = 16$). Mortalities of bighorn sheep were assigned as “probable” kills by mountain lions when two or more of these characteristics were present: tracks; drag marks; or feces from mountain lions; puncture wounds or hematomae on the neck; presence of an intact rumen, ribs cleanly cut as by carnassial teeth; and caching of the carcass. Where possible, location of a kill site was marked with a hand-held GPS (Model 12 XL, Garmin International Inc., Olathe, Kansas, USA); however, in most instances, location of the cached carcass rather than the kill site was recorded, because tracks, drag marks, or other evidence (e.g., blood, hair) at the kill location often were not detectable on granitic substrates.

We created one risk surface from locations of GPS collars of active mountain lions within winter range of bighorn sheep, and a second risk surface from locations where bighorn sheep were killed or cached by mountain lions; these were based on adaptive-kernel utilization distributions (Home Range Tools for ArcGIS; Rodgers et al. 2007) with a smoothing factor of 80% h_{ref} that prevented polygons within home ranges from fragmenting (Kie 2013). Areas within the winter range that fell outside of the 1% utilization distribution for each risk surface were assigned the minimum value of 1.

Topographic metrics.—We obtained elevation data from 1:24,000-scale, 10-m digital elevation models (DEM; US Geological Society Seamless Data Server; <http://seamless.usgs.gov>, accessed 27 September 2010). Average incident solar radiation was

quantified monthly in winter (January–April), by calculating potential relative radiation, a measure incorporating monthly changes in solar elevation, as well as local shading because of topography (Pierce et al. 2005). We calculated potential relative radiation as the sum of hillshade values for each daylight hour on the 15th day of each month, with solar azimuth and elevation values for that hour (US Naval Observatory; <http://aa.usno.navy.mil/data/docs/AltAz.php>). Terrain ruggedness was calculated with the terrain diversity index of Nicholson et al. (1997). We also calculated a binary value for convexity by comparing the elevation at a location with the average elevation of 10-m pixels within the evaluation radius, differentiating concave drainages (convexity = 0), which are less likely to be used by bighorn sheep, from convex ridgelines (convexity = 1); those features could have an identical terrain-ruggedness value. Positive convexity over 15–30 m likely represents outcroppings or ridges providing enhanced visibility for bighorn (Risenhoover and Bailey 1980) or, more generally, escape terrain at the microhabitat scale of the location of the animal, whereas negative convexity at the 100–150 m macro scale probably indicates proximity to steep slopes and rock outcroppings constituting escape terrain. Terrain ruggedness and convexity were calculated over radii of 15, 20, 30, 100, and 150 m, to elucidate the scale at which bighorn sheep selected for rugged and convex escape terrain (Kie et al. 2002, Maier et al 2005, Bowyer and Kie 2006).

Remote sensing.

Weather.—We obtained daily data for precipitation from 1949 to 2009 from the Bishop Airport, California, USA, (Western Regional Climate Center; <http://wrcc.dri.edu/>) located 25 km from winter range on Wheeler Ridge and 42 km from winter range on

Mount Baxter. Data were summarized by calculating cumulative precipitation for each date, beginning 1 October, for the water year (1 October–30 September), total precipitation for each water year, and departure from the 60-year average (1949–2009) for each water year.

Classification of vegetation and cover.—We used image analysis software (Imagine 2010, ERDAS, Inc., Atlanta, Georgia, USA) to classify vegetation types and calculate vegetation and snow-cover indices from cloud-free Landsat 5 Thematic Mapper (TM; $n = 50$) and Landsat 7 Enhanced Thematic Mapper Images (ETM $n = 7$; collectively “TM” imagery; USGS; <http://edcsns17.cr.usgs.gov/v/NewEarthExplorer>; accessed 2–18 August 2011). Downloaded images were used without post-processing, with geometric and radiometric correction by the USGS Earth Resources Observation and Science (EROS) data center. Imagery employed level 1T correction, with 1-arc second National Elevation Dataset (NED) to correct for spatial errors introduced by steep slopes. We used our knowledge of the study area from ground observations, combined with 1-m resolution, 4-band aerial imagery from National Agriculture Imagery Program (NAIP) collected in 2009 (http://www.atlas.ca.gov/download.html#/casil/imageryBaseMapsLandCover/imagery/naip/naip_2009) to validate geo-referencing of Landsat TM images. The NAIP 2009 imagery also was used to generate the rock cover type at the 1-m scale of those aerial photos.

Sesnie et al. (2010) assessed the utility of evaluating habitat for desert bighorn sheep (*O. C. nelsoni*) with vegetation indices derived from the moderate-resolution imager spectrometer (MODIS; 250-m pixel) and TM (30-m pixel), concluding that

MODIS indices were less degraded by effects of low sun angle and topography, than were those from Landsat TM. Our evaluation of third-order selection combined with the heterogeneity of our study area at a 250-m scale, however, precluded use of the MODIS sensor. Further justification for using Landsat is the availability of TM archives dating from 1982, prior to and spanning the period of "range abandonment" by Sierra Nevada bighorn sheep reported by Wehausen (1996). We obtained vegetation classifications from the US Forest Service Existing Vegetation (EVEG) data layers (<http://www.fs.fed.us/r5/rsl/clearinghouse/gis-download>; image date; 31 August 2001, accessed 8 November 2010). We combined EVEG layers for conifer forest woodland, hardwood forest woodland, and mixed conifer-hardwood woodland into a single tree layer. The EVEG system did not adequately resolve areas with partial canopy closure, often dominated by mountain mahogany or juniper, which EVEG usually classified as "shrub," a classification that also included much of the open shrub habitat where bighorn sheep foraged. We classified a cover type of open canopy tree-shrub using Imagine 2010 and a TM image from 1 May 2006 to adequately characterize this cover type. The resulting classification was validated with NAIP 2009 imagery and our knowledge of the study area from field observations. We combined our open-canopy, tree-shrub layer and the EVEG tree classification into a composite tree-shrub cover type.

Temporal variation in snow and vegetation.—We calculated NDVI and Normalized Difference Snow Index (NDSI; Dozier 1989) from digital number (DN) values of 31 TM images collected 2002–2009. To minimize inclusion of misleading values of NDVI that measured snow and not vegetation, we classified pixels having $NDSI > 0.2$ as snow-covered (Hall 1995) and nullified the non-informative NDVI values

for those pixels. We used the more sensitive NDSI threshold of >0.2 to maximize sensitivity to snow, described by Dozier (1989) as sensitive to detection of alpine snow cover even in shadowed areas in the southern Sierra Nevada.

We calculated NDVI of potential foraging areas after masking pixels ($n = 9,686$) covered by snow ($\text{NDSI} > 0.2$), tree-shrub, or rock. Values of NDVI were converted to categories and masked pixels, which were assumed to have no forage value, assigned the reference NDVI value of zero. The remaining pixels were categorized into three equal bins as “Low” (1), “Medium” (2), and “High” (3) from the remaining 10,378 pixels.

Forage tradeoff.—We evaluated the potential benefit of migration to low-elevation habitat in winter by assessing differences in the quality and quantity of potential forage, as indexed by NDVI at high elevations ($>3,000$ m) and low-elevations ($<2,000$ m) used by bighorn sheep in winter (Fig. 4). Locations used by bighorn sheep were defined by high-quality locations (3-D, DOP <10) from GPS collars deployed during winters of 2002–2007. We assumed those locations were representative of the earlier 1987–1995 period of when disuse of low-elevation winter range was reported (Wehausen 1996), for which no data for telemetry locations were available (Villepique et al. 2011). Telemetry data from a past study (Andaloro and Ramey 1981) indicated use of high- and low-elevation habitats in winter, consistent with contemporary data from GPS collars, thereby supporting the extrapolation of modern GPS data as representative of historic locations used by bighorn sheep at high and low elevations in winter (Villepique et al. 2011).

We used 57 Landsat 5 and Landsat 7 TM scenes (Path 42, Row 34), from 1987 to 1994 and from 2002 to 2009 to assess snow cover (NDSI) and NDVI for pixels used by bighorn sheep in winter. Continuous values for NDVI were calculated after removing

TM pixels covered by tree-shrub, rock, or snow (NDSI >0.2) and, consequently, not indexing available forage. Within-scene comparisons between high and low elevations were essential to detect the weak signal (≤ 0.10 NDVI units) among inherent atmospheric variation (e.g., path radiance, atmospheric attenuation, aerosol-induced distortion), and variation arising from geometric sun angle-illumination (e.g., solar elevation, azimuth angle, viewing angle), as well as sensor calibration, all of which can alter NDVI values across images (Chander and Groeneveld 2009). Our use of heterogeneous Landsat 5 and Landsat 7 sensors added an additional source of between-image measurement error that was mitigated through within-image comparison.

Statistical analyses

Resource-selection modeling.—SAS 9.3 software (SAS Institute, Cary, North Carolina, USA) was used for all statistical analyses. We calculated resource-selection functions (RSFs) for the population using conditional logistic regression (PROC LOGISTIC; SAS Institute Inc. 2011) in a matched-case design (Manly et al. 2002, Boyce 2006, Long et al. 2009, Lendrum et al. 2012), with 10 available random locations per animal location. Matched-case design is particularly appropriate for evaluation of RSFs when resources vary over time (McLoughlin et al. 2009). The logistic model was fit for the population of animals, conditioned upon the temporal window of each TM image, thus fitting the model to temporal variation in vegetation quality and quantity (indexed by NDVI) and snow cover (indexed by NDSI).

Prior to analysis, we re-scaled variables for elevation, potential relative radiation, and terrain ruggedness at all radii (15–150 m), so that a 1-unit change represented 100 units of the change in the raw variable; thus, odds ratios for those variables indicate the

relative odds of selection for each 100-unit change in elevation, potential relative radiation, and terrain ruggedness. Mean, SD, and range for those variables in their original scale are provided in the appendix (Table A1).

Model selection.—We retained candidate variables with absolute values of Pearson correlation <0.60 , and screened for multicollinearity using linear regression diagnostics in SAS 9.3 software (Allison 1999). Candidate models included all possible combinations of non-correlated predictor variables with univariate $P < 0.25$ (Hosmer and Lemeshow 2000). We calculated Akaike's information criterion adjusted for small sample size (AIC_c), ΔAIC_c , and Akaike weights for candidate models where $\Delta AIC_c < 4$, indicating substantial information-theoretic support (Burnham and Anderson 2002). We selected among correlated predictor variables by comparing ΔAIC_c among models differing only in those correlated predictors. We evaluated the relative importance of variables based on their Akaike importance weights, calculated as the sum of Akaike weight across all models that contained a particular variable (Burnham and Anderson 2002). We then calculated model-averaged parameter estimates and unconditional standard errors (SE), thereby incorporating both parameter uncertainty and model-selection uncertainty for each predictor variable (Burnham and Anderson 2004). We determined if model-averaged parameter estimates differed from zero by examining whether the unconditional 95% CI overlapped zero (Monteith et al. 2011).

We used k -fold cross validation with five partitions (Boyce et al. 2002, 2003, 2006, Anderson et al. 2005, Long et al. 2009b) to evaluate predictive strength of the resource-selection functions by withholding a randomly selected 20% test-set of animal and available locations, and estimating model parameters with the remaining locations.

For each of five iterations, the coefficients calculated from the training set were used to calculate RSF values for available locations in the test set, which were then ranked by RSF and assigned to 1 of 10 equal-area bins (i.e., 10-percentile bins). Training-set coefficients were then used to calculate values of RSF for animal (i.e., used) locations in the test set. Animal locations were placed in the bins according to RSF value, and number of locations summed for each bin. We regressed the count of animal locations in each bin versus the median value from random points, and used coefficient of determination, slope, and Spearman rank correlations, averaged among the five-fold validation groups, as diagnostic of the predictive success of each model (Boyce et al. 2002, Long et al. 2009b).

Forage tradeoffs.—We compared NDVI at low elevations (<2,000 m) with NDVI at high elevations (>3,000 m) when ≥ 10 snow-free pixels used by bighorn sheep were available in each elevation category within a TM scene, to ensure an adequate sample of potential forage. Within each TM scene, mean NDVI was calculated among snow-free, low-elevation pixels used by bighorn sheep and among snow-free, high-elevation pixels used by bighorn sheep and not classified as rock or tree-shrub. We calculated NDVI tradeoff as the difference of mean low-elevation NDVI minus mean high-elevation NDVI for each TM image and assigned precipitation to-date, total precipitation by water year, and total precipitation in the prior water year to each TM image. We calculated the mean NDVI across 202–1,396 snow-free, low-elevation pixels, and 10–696 snow-free, high-elevation pixels, and calculated NDVI tradeoff as the difference between mean low-elevation NDVI minus mean high-elevation NDVI for 51 TM scenes having ≥ 10 snow-free pixels at high and low elevation.

We compared the NDVI tradeoff between years of above-average precipitation, with the NDVI tradeoff in those years of below-average precipitation with the nonparametric Wilcoxon signed-rank test for median difference, Conover1999), to account for small samples of snow-free pixels present at high elevation during above-average snow years. We explored the relationship among the NDVI tradeoff and cumulative precipitation to-date, total precipitation for the contemporaneous water year, and cumulative precipitation for the prior water year, through linear regression.

Results

Average annual precipitation from 1949 to 2009 was 13.3 cm (Fig. 4). Precipitation was highly variable (CV = 59%) over the 61 years for which data were available, and exceptionally variable (CV = 73%) during 2002–2007, when GPS data were collected from collared bighorn sheep. The driest (2002; 3.5 cm) and third-wettest (2005; 28.5 cm) years on record occurred during that period, demonstrating extremes in snow cover and resource selection by bighorn sheep during drought and wet years (Fig. 5).

We deployed GPS collars on 28 individual bighorn sheep (19 female, 9 male) and collected a mean of 79 days (SD = 49.2 days, range = 10–172 days) of locations in winter. Data met the assumption of independence among animals; no pairs of GPS collars deployed on bighorn sheep were associated (<200 m) for >25% of locations. Thirty-nine GPS collars (including replacement collars) were fitted to 24 individual mountain lions (12 female: 12 male; mean number of fixes 1,094, SD = 1,046, range = 65–4,304 fixes). All but two of 22 mountain lions (12 females and 10 males) used winter ranges of bighorn sheep at Wheeler Ridge ($n = 13$) or Mount Baxter ($n = 7$), and two

mountain lions overlapped both winter ranges. Active locations comprised 47.9% of 5,453 GPS locations within winter ranges of bighorn sheep.

Risk of predation by mountain lions, quantified by the risk surface of locations of active lions (Fig. 6.), was negatively correlated with elevation ($r = -0.73$; Table A2); consequently, candidate models included either one, but not both, predictor variables. The risk surface generated from locations where mountain lions killed and cached bighorn sheep was moderately correlated with the risk surface from active lions ($r = 0.59$; Fig. 6) and elevation ($r = -0.46$; Table A2); accordingly, both variables measuring risk from mountain lions were included as candidate predictors for modeling RSFs.

Results of RSF modeling indicated selection for the risk surface quantifying probability of mountain lion activity as one the strongest predictor variables; (i.e., Akaike importance weight = 1.0; Table 2; Fig. 7). Although both sexes of bighorn selected for that measure of risk of predation by mountain lions, selection was nearly twice as strong for males ($\beta = 2.3 \times 10^{-2}$) as for females ($\beta = 1.2 \times 10^{-2}$), with non-overlapping confidence intervals (Table 2). Selection for areas used by active mountain lions was a better predictor of resource selection during winter than was selection for lower elevations ($\Delta AIC_c = 73.7$ for females, $\Delta AIC_c = 124.1$ for males; Table 3).

Additional predictors having the strongest level of support in all candidate models (i.e., Akaike importance weight = 1.0; Table 2) for the sexes of bighorn sheep included positive selection for areas of high solar radiation, steep slopes, and proximity to rugged terrain, which differed in scale by sex (150 m for females, 100 m for males; Fig. 7). Our methods prevented simultaneous evaluation to determine relative strength of the correlated metrics of ruggedness at 100-m and 150-m scales ($r = 0.87$; Table A2). All

candidate models for females included an additional predictor, avoidance of snow (i.e., negative selection for NDSI), whereas candidate models for males indicated avoidance of tree-shrub cover (Akaike importance weight = 0.97; Table 2; Fig. 7).

Model fit was improved by inclusion of less influential variables including the rock cover type, avoided by both sexes of bighorn, whereas females selected for convexity at the 15-m scale, avoided ruggedness at the 30-m scale, and avoided convexity at the 150-m scale; males selected for ruggedness at the 20-m scale, but avoided convexity at the 100-m scale (Fig. 7). Masking temporally varying snow cover, static tree-shrub, and rock cover types for non-informative NDVI values, collectively accounted for 49.9% of 18,240 available locations in our data set. Vegetation conditions, as indexed by NDVI at the remaining 50.1% of locations, relative to reference areas of rock, snow or tree-shrub, did not enter RSF models. Results of *k*-fold cross-validation for RSF models indicated robust fit and substantial accuracy of prediction by models for female and male bighorn sheep (Table 4).

Forage tradeoff was evaluated with high-quality locations from GPS collars that identified TM pixels used by bighorn sheep in winter at high elevation ($n = 1,272$ locations; $n = 720$ unique TM pixels) and low elevation ($n = 3,830$ locations; $n = 1,396$ unique pixels). Values of NDVI pooled across TM images showed high variability, and were inconclusive in assessing a potential trade-off between low-elevation vegetation and high-elevation vegetation condition in drought years compared with wet years (Fig. 8A). When data were analyzed by comparison of the median of differences between low-elevation habitat and those at high elevations within TM images, however, a significant tradeoff in NDVI was demonstrated for years of above average precipitation compared

with years of below average precipitation (Fig. 8B; Wilcoxon statistic = 589, $P < 0.001$). The best single predictor of the magnitude of an NDVI tradeoff was precipitation to-date (Fig. 9). Additional variation was explained (R^2 adjusted = 0.51) by addition of precipitation in the prior water year, yielding the linear equation: $NDVI\ tradeoff = 0.017 + 0.0030 \times (\text{precipitation to-date}) + 0.0013 \times (\text{precipitation in prior water year})$.

DISCUSSION

Hypothesis I-A; Resource selection was influenced by direct risk of predation

Challenges to assessing the influence of direct risk of predation included the choice of appropriate spatial and temporal scales. We quantified direct risk of predation with a static probability-density function generated from the aggregate of locations of active mountain lions over eight winters. Such a metric allowed evaluation of resource selection by bighorn sheep relative to generalized predation risk, but did not attempt to quantify short-term responses to transient risk, which are evident in correlation of locations of bighorn sheep and mountain lions, when viewed in a temporal window of days (J. T. Villepique, *unpublished data*). Although mountain lions are protected in California (Torres 1996), individual mountain lions were removed from the Mount Baxter and Wheeler Ridge winter ranges, following identical protocols, over the span of this study. Removal of those mountain lions identified as a threat to endangered bighorn sheep may have reduced the influence of those mountain lions more likely to hunt bighorn sheep on the probability distribution generated from GPS-collared mountain lions.

The hypothesis predicting an influence by direct risk of predation on resource selection by male and female Sierra Nevada bighorn sheep (Table 1) was supported, but

in a direction opposite to that predicted under the predation risk hypothesis. One of the strongest positive predictors of resource selection by bighorn sheep was a measure of direct risk of predation by mountain lions; all candidate models (i.e., Akaike importance weight = 1.0) for female and for male bighorn sheep included selection for proximity to locations where mountain lions were active (Fig. 7; Table 2), and likely hunting (Knopff 2010). This outcome was probably a result of bighorn sheep selecting areas with suitable forage and escape terrain, and mountain lions hunting in areas where mule deer overlapped winter range of bighorn sheep (Villepique et al. 2011, Johnson et al. 2013). This outcome also was consistent with the determination by Pierce et al. (2000) that the distribution of mountain lions was predicated upon the distribution of ungulates available to hunt. Greene (2010) also reported positive selection for areas of high use by mountain lions on the Mount Baxter winter range, in her assessment of a cohort of Sierra Nevada bighorn sheep collared in 2007–2008.

Hypothesis I-B; Resource selection was strongly influenced by indirect risk of predation

Evaluation of resource selection by bighorn sheep, relative to habitat-mediated, indirect risk of predation, presented challenges related to biases inherent in GPS collars, which are less likely to obtain high-quality fixes when proximity to escape terrain blocks available sky. Difficulties also arose in differentiating qualitative differences within the rock cover type, present at only 1.7% of random points (Table A1). Rock cover was associated with steep escape terrain used by bighorn sheep in our study area, but also included massive granitic plutons, favored by human technical rock climbers, which were too steep for bighorn sheep to traverse. Our analysis of resource selection also did not

account for effects of sociality, specifically group size, an important determinant of foraging decisions under risk of predation in bighorn sheep (Berger 1978, Mooring 2004, Schroeder et al. 2010).

The hypothesis positing influence of indicators of indirect risk of predation was supported by selection of rugged topographic features conferring protection from some predators. All models of RSF for the sexes indicated significant selection for steep slopes and selection for proximity to escape terrain (Table 2; Fig. 7). Differences in scale among the sexes likely were related to group size (Berger 1978, Mooring 2004, Schroeder et al. 2010). The indirect-risk hypothesis received additional support from improved model fit when measures of ruggedness and convexity in immediate proximity to the animal were added to RSFs (Table 2, Fig. 7). An unexpected result was that females selected against ruggedness at the intermediate 30-m scale, albeit with weak evidence (Akaike importance weight = 0.09). Rachlow and Bowyer (1998) similarly documented selection of less-rugged microhabitats, proximate to rugged escape terrain, by female Dall's sheep (*Ovis dalli*). Proximity to escape terrain (represented by the strongly selected ruggedness within 150 m) likely mitigated indirect predation risk for female bighorn sheep in our study (Table 2, Fig. 7). A remaining corollary supporting the indirect risk hypothesis was the avoidance of tree-shrub cover by males although, surprisingly, not by females, possibly because availability of tree-shrub cover was lower at mid-elevations occupied by females compared with riparian and shrub areas proximate to the lowest elevations, used exclusively by males. Another unexpected outcome was avoidance of the rock cover-type by both sexes. This outcome was best explained by inclusion of large areas of steep cliffs inaccessible to bighorn in that cover type.

Hypothesis II; Habitat selection is strongly influenced by forage availability

Application of satellite NDVI as a metric for spatial and temporal patterns of forage condition within the home range (i.e., third-order selection, Johnson 1980) was problematic in our study area. A matrix of rock, trees, and snow, where NDVI is non-informative for indexing forage conditions, is common at the spatial scale of available satellite sensors (Pettorelli et al 2005). Those cover types composed 49.9% of available locations in the TM images we used. Consequently, one-half of pixels were assigned the reference NDVI value of zero, reducing the power to detect selection among the remaining categories of NDVI.

We also did not post-process TM images to convert raw radiance to reflectance, decreasing the power to detect variation in NDVI. Application of those computationally intensive radiometric corrections for each image entails an added layer of complexity when heterogeneous sensors are used (e.g., Landsat 5 TM and Landsat 7 ETM), but is essential for temporal comparisons among images (e.g., Sesnie et al. 2010). Our analyses, however, did not make between-image comparisons, because RSFs were calculated with “used” versus “available” locations conditioned within the common temporal window of the TM scene, thereby reducing the need for corrections.

The forage-availability hypothesis was supported by significant selection in all candidate models for potential relative radiation, a proxy for insolation that is correlated with patterns of vegetation growth (Pierce et al. 2005). Similarly, females, but not males, avoided snow cover (i.e., selected for negative NDSI), as predicted by the forage-availability hypothesis. Models of resource selection did not, however, include NDVI as an informative predictor. Despite shortcomings in the application of TM imagery to

evaluate forage in a use versus availability model at the scale of third-order selection, we successfully used radiance values from TM sensors to elucidate strong avoidance of snow cover by females (i.e., females selected for negative NDSI). Males, however, sometimes remained in snow-covered, high-elevation areas rather than moving to lower elevations (J. T. Villepique, *personal observations*), as was typical for females. This divergent strategy relative to snow was likely related to the larger body size of males (Geist 1971), allowing movement and foraging in snow at a lower cost, relative to that for smaller-bodied females. Schroeder et al. (2010) established that male bighorn sheep in the Sierra Nevada selected areas with significantly higher biomass of shrubs and consumed significantly greater proportions of sagebrush than did females. Those results are consistent with size differences between male and female digestive systems (Barboza and Bowyer 2001, 2002), allowing males to use lower-quality woody forage emerging from snow, whereas females would have more difficulty doing so.

Hypothesis III; Tradeoff between forage versus risk of predation was reduced during drought

Locations used by bighorn sheep at high elevation (>3,000 m) during winter often were covered by snow during years of above-average precipitation, leaving a limited number of snow-free pixels in wind-blown or south-facing areas. Consequently, forage conditions could be indexed by NDVI only in small samples of pixels within TM scenes, yielding additional variation to inherent variability among TM scenes (Fig 9).

Application of within-scene comparisons of NDVI, calculated from uncorrected TM radiance, however, nullified temporal variation among NDVI values, and allowed

comparison of forage tradeoff at static high and low-elevation locations used by bighorn sheep in winter.

The hypothesis that drought reduced the forage benefit of migration to low elevations was supported; significantly greater forage benefits resulted from migration to low elevations, where predation risk was highest, in above-average precipitation years compared with the benefits accrued in lower than average precipitation years. Differences in vegetation condition, as indexed by NDVI at low-elevation locations used by bighorn sheep minus NDVI at high-elevation locations used by bighorn sheep, were greatest in years with above-average precipitation (Fig. 8B). The NDVI tradeoff had a positive linear relationship with quantity of precipitation, with variation largely explained (R^2 adjusted = 0.51) by cumulative precipitation to-date and precipitation the prior water year (Fig. 9). The greatest forage benefit of migration, therefore, accrued in sequential years having above-average precipitation, while the lowest benefit was present in consecutive drought years.

Wehausen (1992) concluded that it was the timing, rather than quantity, of precipitation that best correlated with crude protein content in bighorn sheep feces, a proxy for dietary quality (Leslie et al. 2008). His investigation at Mount Baxter, however, identified a measure of Julian date itself as explanatory of most variation in fecal crude protein ($R^2 = 0.57$; Wehausen 1992), and went on to conclude that the best single predictor ($R^2 = 0.78$) of fecal crude protein was the number of days elapsed after a substantial precipitation event, termed, “the initiating storm” (Wehausen 1992). This conclusion is suspect, however, as this measure was predicated on the occurrence of a storm event of sufficient magnitude (i.e., quantity of precipitation), defined by Wehausen

(1992) as having, “initiated perennial grass growth,” simultaneously the predictor and predicted.

Our models of RSF by bighorn sheep were robust because of pooling of data among heterogeneous winter ranges at Mount Baxter and Wheeler Ridge, and because the years 2002–2007, when data were collected from GPS-collars, were characterized by highly variable precipitation. The driest (2002) and wettest (2005) years since 1987, when Wehausen (1996) reported the disuse of low-elevation winter range, occurred during this 6-year span. Wehausen (1996) asserted that that use of low-elevation habitat in winter was the rule, unaffected by sequential years of drought, but this is not consistent with our data (Fig. 5) or past observations (Andaloro and Ramey 1981).

In our study, one of the strongest positive predictors of resource selection by Sierra Nevada bighorn sheep was a measure of direct risk of predation by mountain lions, implicating the activity of mountain lions as a strong predictor of habitat selection by Sierra Nevada Bighorn Sheep—as posited by Wehausen (1996)—but in the opposite direction he suggested. Our analysis demonstrated that rather than abandon preferred habitat, bighorn sheep continued to select the same areas where mountain lions actively hunted in bighorn sheep winter range (Fig. 6). We established an alternative to the notion of predator-induced range abandonment (Wehausen 1996), by contrasting forage tradeoff in wet versus dry years, revealing significantly reduced benefits of migration to low elevation in drought years (Fig. 8). The period of “range abandonment” (Wehausen 1996) occurred during a period of 6 consecutive years of drought (1987–1992; Roos 1992) when snow cover, which was avoided by female bighorn sheep, was sparse at high

elevations, and forage benefits of migration to low elevation were significantly lower than in years of above-average precipitation.

Top-down effects, in the form of removal by helicopter capture for translocation, however, may have played a part in the proposed range abandonment in addition to the role of drought as a bottom-up driver. Intensive helicopter capture and removal of 103 bighorn sheep on low elevation winter range at Mount Baxter (Bleich et al. 1990b, Wehausen 1996) preceded the 1987–1995 period of proposed range abandonment (Wehausen 1996). Those captures not only preceded, but indeed continued into March 1988, when eight female and three male bighorn sheep were removed (Bleich et al. 1990b) from the low-elevation range that Wehausen (1996) inexplicably defined as then “abandoned.” Helicopter capture and translocation was analogous to “direct predation,” in that the result of removing animals continuing to use low-elevation winter range was to leave only those animals using a parallel strategy of overwintering at high elevation. Furthermore, while short-term disturbance and flight responses by mountain sheep are well documented in response to low-level helicopter flights (Bleich et al. 1990, 1994, Stockwell 1991, Frid 2003), cumulative effects of repeated helicopter captures are unknown. Repeated helicopter captures that remove conspecifics may alter behavior and elicit responses analogous to those behaviors that mitigate indirect risk of predation; avoidance of areas lacking escape terrain, such as those low-elevation areas subject to recurrent helicopter captures. More research is warranted to elucidate behavioral responses to repeated helicopter capture efforts, especially for this endangered taxon.

Our alternative bottom-up hypothesis is supported by data demonstrating a reduced tradeoff by bighorn sheep remaining in snow-free, high-elevation winter habitat

during drought years, providing an empirically and theoretically consistent explanation free from the inconsistencies of the predator-induced hypothesis of range abandonment. The bottom-up explanation resolves the inherent conflict between the range-abandonment hypothesis and the theory of natural selection: maladaptive behaviors cannot persist in natural systems. Mountain lions share millennia of sympatry with bighorn sheep in North America (Cowan 1940, Culver et al. 2000), while hydroclimatic reconstruction demonstrates the non-uniqueness of severe drought (Cook et al. 2004) over the same period. Thus, evidence does not support a novel set of conditions during the 1987–1995 period of range-abandonment. The proposition that predator-induced range abandonment led to demographic catastrophe fundamentally conflicts with the concept of an ESS (Maynard Smith and Price 1973) for resource selection by bighorn sheep under risk of predation by a non-novel predator, the mountain lion. If avoidance of low-elevation winter range was, on average, more costly in terms nutritional trade off, energetic demands, or risks of stochastic mortality inherent to life at high elevation in winter (Wehausen 1996), compared with use of low-elevation winter range, such a strategy would experience strong negative selection. Natural selection would favor adoption of a “cheater” strategy, wherein some animals make use of low-elevation winter range and benefit from nutritious forage, while avoiding of the perils of life at high elevation. Survivors among these “cheaters” would be strongly selected for. To support the claim that Sierra Nevada bighorn sheep responded to risk of predation by avoiding resources critical to survival and reproduction (e.g., low-elevation habitat in winter; Wehausen 1996) in a manner incompatible with an ESS, extraordinary evidence is necessary, but remains lacking.

The bottom-up hypothesis explaining avoidance of low-elevation winter range by bighorn sheep is consistent with the findings of Kucera (1988), and Pierce et al. (2012), which documented drought-induced reduction in forage available to mule deer wintering in Round Valley, concurrent with the hypothetical predator-induced range abandonment by bighorn sheep (Wehausen 1996). The winter range of the Round Valley mule deer herd overlapped one-third of the winter range of bighorn sheep at Wheeler Ridge (Villepique et al. 2011). Kucera (1988) concluded that drought and limited availability of forage in winter, and not predation by mountain lions, caused the 50% decline in the number of mule deer wintering adjacent to Wheeler Ridge during 1985–1988. Pierce et al. (2012) analyzed long-term demographic and physiological conditions in this mule deer population during 1984–1998, and concluded that bottom-up processes, including prolonged drought, regulated mule deer populations through 1990, when the mule deer population began to recover. Diets of mule deer were dominated by bitterbrush (Kucera 1988, 1997), also a major forage species for bighorn sheep in winter (Wehausen 1980). Kucera noted an absence of leader growth in bitterbrush during the 1986–1987 drought, as well as heavily browsed shrubs and frequent observations of mule deer feeding while standing on hind legs to reach bitterbrush leaves (Kucera 1988). In the absence of data refuting density-dependent, drought-induced, limits to forage as the major factor responsible for declines in Sierra Nevada bighorn sheep and elevational shifts in use of winter range (Wehausen 1996), bottom-up processes offer a stronger alternative explanation for the observed pattern.

Investigations into effects of behavioral responses to risk of predation in large herbivores have yielded diverse results, leaving many unanswered questions regarding

the applicability and magnitude of effects from trait-mediated, indirect interactions (Abrams 1995) in terrestrial systems. Ripple et al (2001) reported a behaviorally mediated trophic cascade (BMTC) in elk in the Greater Yellowstone Ecosystem (hereafter, “Yellowstone”), wherein elk responded to risk of predation by wolves by avoiding risky stands of quaking aspen (*Populus tremuloides*), thereby reducing herbivory and allowing increased recruitment of aspens. Kauffman et al. (2010) evaluated evidence for a BMTC of sufficient magnitude to structure aspen communities in Yellowstone, by assessing foraging by elk under risk of predation by wolves, and by comparing historical aspen recruitment inside and outside of exclosures, and concluded that historic precipitation and number of elk, and not a BMTC, explained recruitment of aspen.

Similar conflicting results characterize studies of physiological and demographic costs accrued from energetic demands of antipredator behavior. Creel et al. (2007) investigated the correlation between risk of predation by wolves and recruitment in elk in the Yellowstone system, with results indicating a negative relationship between predation risk and reproduction. Middleton et al. (2013), conversely, detected no significant effects on pregnancy or body condition in elk subject to frequent proximity and risk of predation by wolves in the Yellowstone system. Those examples illustrate the possibility that conclusions about prey behavior and demography attributed to indirect risk of predation may, upon further examination, be better explained by bottom-up processes and the direct effects of predation. We find such a bottom-up explanation of resource selection by Sierra Nevada bighorn sheep far more plausible, owing to empirical and theoretical

support, than the predator-induced range-abandonment hypothesis proffered by Wehausen (1996).

ACKNOWLEDGMENTS

We thank helicopter pilot S. DeJesus, and California Department of Fish and Wildlife capture specialists R. Teagle and T. Glenner, for safe capture of bighorn sheep, and houndsmen J. Davis and J. Ostergard, and their assistants V. Davis, M. Kiner, M. Leonard-Cahn, and J. Schmalenberger for their work capturing mountain lions. Additional capture support was provided by personnel from the CDFW Wildlife Investigations Laboratory including B. Gonzales, A. Hunter, K. Jones, L. Konde, J. Schultz., P. Swift, and S. Torres. We thank the many employees and volunteers who helped collect data, including C. Baker, L. Bowermaster, K. Ellis, J. Erlenbach, A. Feinberg, J. Fusaro, D. German, L. Greene, D. Jensen, R. Noles, N. Partridge, P. Partridge, C. Schroeder, A. Stephenson, and T. Taylor. Discussions with D. Delehanty, J. Kie, R. Long, C. Peterson, T. Stephenson, and J. Wehausen were valuable in guiding this investigation. This study was funded by California Department of Fish and Wildlife Sierra Nevada Bighorn Sheep Recovery Program, California Deer Association, Desert Bighorn Council, California Chapter of the Wild Sheep Foundation, Department of Biological Sciences at Idaho State University, and the Institute of Arctic Biology at the University of Alaska Fairbanks.

This is a contribution from the Sierra Nevada Bighorn Sheep Recovery Program and is Professional Paper XXX from the Eastern Sierra Center for Applied Population Ecology.

LITERATURE CITED

- Abrams, P. A. 1995. Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *American Naturalist* 146:112-134.
- Allison, P. D. 1999. Logistic regression using the SAS system: theory and application. SAS Institute, Cary, North Carolina, USA.
- Andaloro, L., and R. R. Ramey. 1981. The relocation of bighorn sheep in the Sierra Nevada of California. University of California, Santa Cruz, Environmental Field Program Publication 7:1-60.
- Anderson, D. P., M. G. Turner, J. D. Forester, J. Zhu, M. S. Boyce, H. Beyer, and L. Stowell. 2005. Scale-dependent summer resource selection by reintroduced elk in Wisconsin, USA. *Journal of Wildlife Management* 69:298-310.
- Arthur, S. M., B. F. J. Manly, L. L. McDonald, and G. W. Garner. 1996. Assessing habitat selection when availability changes. *Ecology* 77:215-227.
- Barboza, P. S., and R. T. Bowyer. 2000. Sexual segregation in dimorphic deer: a new gastrocentric hypothesis. *Journal of Mammalogy* 81:473-489.
- Barboza, P. S., and R. T. Bowyer. 2001. Seasonality of sexual segregation in dimorphic deer: extending the gastrocentric model. *Alces* 37:275-292.
- Barboza, P. S., K. L. Parker, and I. D. Hume. 2009. Integrative wildlife nutrition. Springer Verlag, Berlin, Germany.
- 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.

- Beck, P. S. A., T. J. Wang, A. K. Skidmore, and X. H. Liu. 2008. Displaying remotely sensed vegetation dynamics along natural gradients for ecological studies. *International Journal of Remote Sensing* 29:4277-4283.
- Belovsky, G. E. 1984. Herbivore optimal foraging: a comparative test of three models. *American Naturalist* 124:97-115.
- Berger, J. 1978. Group size, foraging, and antipredator ploys: an analysis of bighorn sheep decisions. *Behavioral Ecology and Sociobiology* 4:91-100.
- 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., J. E. Swenson, and I.-L. Persson. 2001. Recolonizing carnivores and naive prey: conservation lessons from Pleistocene extinctions. *Science* 291:1036-1039.
- Bertram, B. C. R. 1978. Living in groups: predators and prey. Pages 64-96 *in* Krebs, J. R., and N. B. Davies, editors. *Behavioural ecology: an evolutionary approach*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Beyer, H. 2005. Hawth's analysis tools for ArcGIS. <http://spatialecology.com/htools/>
- Bleich, V. C. 1999. Mountain sheep and coyotes: patterns of predator evasion in a mountain ungulate. *Journal of Mammalogy* 80:283-289.
- Bleich, V. C., R. T. Bowyer, A. M. Pauli, M. C. Nicholson, and R. W. Anthes. 1994. Mountain sheep *Ovis canadensis* and helicopter surveys: ramifications for the conservation of large mammals. *Biological Conservation* 70:1-7.

- Bleich, V. C., R. T. Bowyer, A. M. Pauli, R. L. Vernoy, and R. W. Anthes. 1990a. Responses of mountain sheep to helicopter surveys. *California Fish and Game* 76:197-204.
- Bleich, V. C., R. T. Bowyer, and J. D. Wehausen. 1997. Sexual segregation in mountain sheep: resources or predation? *Wildlife Monographs* 134:1-50.
- Bleich, V. C., J. D. Wehausen, K. R. Jones, and R. A. Weaver. 1990b. Status of bighorn sheep in California, 1989 and translocations from 1971 through 1989. *Desert Bighorn Council Transactions* 34:24-26.
- Bowyer, R. T. 2004. Sexual segregation in ruminants: definitions, hypotheses, and implications for conservation and management. *Journal of Mammalogy* 85:1039-1052.
- Bowyer, R. T., and J. G. Kie. 2006. Effects of scale on interpreting life-history characteristics of ungulates and carnivores. *Diversity and Distributions* 12:244-257.
- Bowyer, R. T., J. G. Kie, and V. Van Ballenberghe. 1998. Habitat selection by neonatal black-tailed deer: climate, forage, or risk of predation? *Journal of Mammalogy* 79:415-425.
- Boyce, M. S. 2006. Scale for resource selection functions. *Diversity and Distributions* 12:269-276.
- Boyce, M. S., P. R. Vernier, S. E. Nielsen, and F. K. A. Schmiegelow. 2002. Evaluating resource selection functions. *Ecological Modeling* 157:281-300.

- Boyce, M. S., J. S. Mao, E. H. Merrill, D. Fortin, M. G. Turner, J. Fryxell, and P. Turchin. 2003. Scale and heterogeneity in habitat selection by elk in Yellowstone National Park. *Ecoscience* 10:421-431.
- Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385-399.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multi-model inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33:261-304.
- Cain, J. W., P. R. Krausman, B. D. Jansen, and J. R. Morgart. 2005. Influence of topography and GPS fix interval on GPS collar performance. *Wildlife Society Bulletin* 33:926-934.
- Chander, G., and D. P. Groeneveld. 2009. Intra-annual NDVI validation of the Landsat 5 TM radiometric calibration. *International Journal of Remote Sensing* 30:1621-1628.
- Conover, W. J. 1999. Practical nonparametric statistics. John Wiley and Sons, New York, New York, USA.
- Cowan, I. M. 1940. Distribution and variation in the native sheep of North America. *American Midland Naturalist* 24:505-580.
- Creel, S., and D. Christianson. 2008. Relationships between direct predation and risk effects. *Trends in Ecology and Evolution* 23:194-201.

- Creel, S., D. Christianson, S. Liley, and J. A. Winnie. 2007. Predation risk affects reproductive physiology and demography of elk. *Science* 315:960.
- Culver, M., W. E. Johnson, J. Pecon-Slattery, and S. J. O'Brien. 2000. Genomic ancestry of the American puma (*Puma concolor*). *Journal of Heredity* 91:186-197.
- D'Eon, R. G., and D. Delparte. 2005. Effects of radio-collar position and orientation on GPS radio-collar performance, and the implications of PDOP in data screening. *Journal of Applied Ecology* 42:383-388.
- Dozier, J. 1989. Spectral signature of alpine snow cover from the Landsat Thematic Mapper. *Remote Sensing of Environment* 28:9-22.
- Farmer, C. J., D. K. Person, and R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management* 70:1403-1415.
- 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., T. Coulson, J. M. Gaillard, J. T. Hogg, and F. Pelletier. 2006. Stochastic predation events and population persistence in bighorn sheep. *Proceedings of the Royal Society B: Biological Sciences* 273:1537-1543.
- 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 B: Biological Sciences* 365:2187-2200.
- Frair, J. L., S. E. Nielsen, and E. H. Merrill. 2004. Removing GPS collar bias in habitat selection studies. *Journal of Applied Ecology* 41:201-212.

- Frid, A. 1997. Vigilance by female Dall's sheep: interactions between predation risk factors. *Animal Behaviour* 53:799-808.
- Frid, A. 2003. Dall's sheep responses to overflights by helicopter and fixed-wing aircraft. *Biological Conservation* 110:387-399.
- Fryxell, J. M., J. Greever, and A. R. E. Sinclair. 1988. Why are migratory ungulates so abundant? *American Naturalist* 131:781-798.
- Geist, V. 1971. Mountain sheep. A study in behavior and evolution. University of Chicago Press., Chicago, Illinois, USA.
- Greene, L. 2010. Short-term effects of wildfire on Sierra Nevada bighorn sheep habitat ecology. M.S. Thesis. University of Montana, Missoula, Montana, USA.
- Hamel, S., M. Garel, M. Festa-Bianchet, J.-M. Gaillard, and S. D. Cote. 2009. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *Journal of Applied Ecology* 46:582-589.
- Hamilton, W. D. 1971. Geometry for the selfish herd. *Journal of Theoretical Biology* 31: 295-311.
- Hansen, B. B., I. Herfindal, R. Aanes, B.-E. Saether, and S. Henriksen. 2009. Functional response in habitat selection and the tradeoffs between foraging niche components in a large herbivore. *Oikos* 118:859-872.
- Hayes, C. L., E. S. Rubin, M. C. Jorgensen, R. A. Botta, and W. M. Boyce. 2000. Mountain lion predation of bighorn sheep in the Peninsular Ranges, California. *Journal of Wildlife Management* 64:954-959.

- 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.
- Hosmer, D. W., and S. Lemeshow. 2000. *Applied logistic regression*. John Wiley and Sons, New York, New York, USA.
- 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. 2013. Evaluating apparent competition in limiting the recovery of an endangered ungulate. *Oecologia* 171:295-307.
- Kauffman, M. J., Brodie, J. F., and E. F. Jules. 2010. Are wolves saving Yellowstone's aspen? A landscape-level test of a behaviorally mediated trophic cascade. *Ecology* 91:2742–2755.
- Kie, J. G. 1999. Optimal foraging and risk of predation: effects on behavior and social structure in ungulates. *Journal of Mammalogy* 80:1114-1129.
- Kie, J. G. 2013. A rule-based ad hoc method for selecting a bandwidth in kernel home-range analyses. *Animal Biotelemetry* 1:13.
- Kie, J. G., R. T. Bowyer, M. C. Nicholson, B. B. Boroski, and E. R. Loft. 2002. Landscape heterogeneity at differing scales: effects on spatial distribution of mule deer. *Ecology* 83:530-544.
- Kilpatrick, H. J., A. J. DeNicola, and M. R. Ellingwood. 1996. Comparison of standard and transmitter-equipped darts for capturing white-tailed deer. *Wildlife Society Bulletin* 24:306-310.

- Knopff, K. H., A. A. Knopff, M. B. Warren, and M. S. Boyce. 2009. Evaluating global positioning system telemetry techniques for estimating cougar predation parameters. *Journal of Wildlife Management* 73:586-597.
- Knopff, K. H. 2010. Cougar predation in a multi-prey system in west-central Alberta. Ph.D. Dissertation, University of Alberta, Edmonton, Alberta, Canada.
- Krausman, P. R., J. J. Herver, and L. L. Ordway. 1985. Capturing deer and mountain sheep with a net-gun. *Wildlife Society Bulletin* 13:71-73.
- Kruuk, H. 1972 . The spotted hyena: a study of predation and social behavior. University of Chicago Press, Chicago, Illinois, USA.
- Kucera, T. E. 1988. Ecology and population dynamics of mule deer in the eastern Sierra Nevada, California. Ph.D. Dissertation. University of California, Berkeley, California, USA.
- Kucera, T. E. 1997. Fecal indicators, diet, and population parameters in mule deer. *Journal of wildlife management* 61:550-560.
- Lendrum, P. E., C. R. Anderson Jr., R. A. Long, J. G. Kie, and R. T. Bowyer. 2012. Habitat selection by mule deer during migration: effects of landscape structure and natural-gas development. *Ecosphere* 3:art82.
- 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.

- Leslie, D. M., Jr., R. T. Bowyer, and J. A. Jenks. 2008. Facts from feces: nitrogen still measures up as a nutritional index for mammalian herbivores. *Journal of Wildlife Management* 72:1420-1433.
- Lima, S. L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *Bioscience* 48:25-34.
- Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68:619-640.
- Long, R. A., J. G. Kie, R. T. Bowyer, and M. A. Hurley. 2009a. Resource selection and movements by female mule deer *Odocoileus hemionus*: effects of reproductive stage. *Wildlife Biology* 15:288-298.
- Long, R. A., J. D. Muir, J. L. Rachlow, and J. G. Kie. 2009b. A comparison of two modeling approaches for evaluating wildlife habitat relationships. *Journal of Wildlife Management* 73:294-302.
- MacArthur, R. H., and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100:603-609.
- Maier, J. A. K., J. M. Ver Hoef, A. D. McGuire, R. T. Bowyer, L. Saperstein, and H. A. Maier. 2005. Distribution and density of moose in relation to landscape characteristics: effects of scale. *Canadian Journal of Forest Resources* 33:2233-2243.
- Manly, B. F. J., L. L. McDonald, D. L. Thomas, T. L. McDonald, and W. P. Erickson. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer, Dordrecht, The Netherlands.

- Maynard Smith, J., and G. R. Price. 1973. The logic of animal conflict. *Nature* 246:15-18.
- McCann, L. J. 1956. Ecology of the mountain sheep. *American Midland Naturalist* 56:297-324.
- McLoughlin, P. D., D. W. Morris, D. Fortin, E. Vander Wal, and A. L. Contasti. 2009. Considering ecological dynamics in resource selection functions. *Journal of Animal Ecology* 79:4-12.
- McNaughton, S. J. 1985. Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs* 55:259-294.
- Middleton, A. D., M. J. Kauffman, D. E. McWhirter, M. D. Jimenez, R. C. Cook, J. G. Cook, S. E. Albeke, H. Sawyer, and P. J. White. 2013. Linking anti-predator behaviour to prey demography reveals limited risk effects of an actively hunting large carnivore. *Ecology Letters* 16:1023-1030.
- Molvar, E. M., and R. T. Bowyer. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. *Journal of Mammalogy* 75:621-630.
- Mooring, M. S., T. A. Fitzpatrick, and T. T. Nishihira. 2004. Vigilance, predation risk, and the Allee effect in desert bighorn sheep. *Journal of Wildlife Management* 68:519-532.
- Monteith, K. L., V. C. Bleich, T. R. Stephenson, B. M. Pierce, M. M. Conner, R. W. Klaver, and R. T. Bowyer. 2011. Timing of seasonal migration in mule deer: effects of climate, plant phenology, and life-history characteristics. *Ecosphere* 2:art47.

- Monteith, K.L., V.C. Bleich, T.R. Stephenson, B.M. Pierce, M.M. Conner, J.G. Kie, and R.T. Bowyer. 2014. Life-history characteristics of mule deer: effects of nutrition in a variable environment. *Wildlife Monographs* 186:1-56.
- Montgomery, R. A., G. J. Roloff, and J. M. Ver Hoef. 2011. Implications of ignoring telemetry error on inference in wildlife resource use models. *Journal of Wildlife Management* 75:702-708.
- 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.
- Oehlers, S. A., R. T. Bowyer, F. Huettmann, D. K. Person, and W. B. Kessler. 2011. Sex and scale: implications for habitat selection by Alaskan moose *Alces alces gigas*. *Wildlife Biology* 17:67-84.
- 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 and Evolution* 20:503-510.
- Pettorelli, N., F. Pelletier, A. V. Hardenberg, M. Festa-Bianchet, and S. D. Cote. 2007. Early onset of vegetation growth versus rapid green-up: impacts on juvenile mountain ungulates. *Ecology* 88:381-390.
- Pierce, B. M., V. C. Bleich, and R. T. Bowyer. 2000. Social organization of mountain lions: does a land-tenure system regulate population size? *Ecology* 81:1533-1543.
- Pierce, B. M., V. C. Bleich, and C.-L. B. Chetkiewicz. 1998. Timing of feeding bouts of mountain lions. *Journal of Mammalogy* 79:222-226.

- Pierce, B. M., V. C. Bleich, K. L. Monteith, and R. T. Bowyer. 2012. Top-down versus bottom-up forcing: evidence from mountain lions and mule deer. *Journal of Mammalogy* 93:977-988.
- Pierce, K. B., T. Lookingbill, and D. Urban. 2005. A simple method for estimating potential relative radiation (PRR) for landscape-scale vegetation analysis. *Landscape Ecology* 20:137-147.
- Pyke, G. H. 1984. Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* 15:523-575.
- Quinn, A. C. D., D. M. Williams, and W. F. Porter. 2012. Postcapture movement rates can inform data-censoring protocols for GPS-collared animals. *Journal of Mammalogy* 93:456-463.
- Rachlow, J. L., and R. T. Bowyer. 1994 . Variability in maternal behavior by Dall's sheep: environmental tracking or adaptive strategy? *Journal of Mammalogy* 75:328-337.
- Rachlow, J. L., and R. T. Bowyer. 1998. Habitat selection by Dall's sheep (*Ovis dalli*): maternal trade-offs. *Journal of Zoology* 245:457-465.
- Ripple, W. J., E. J. Larsen, R. A. Renkin and D. W. Smith. 2001. Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. *Biological Conservation* 101:277-234.
- Risenhoover, K. L., and J. A. Bailey. 1980. Visibility: an important factor for an indigenous, low-elevation bighorn herd in Colorado. *Symposium of the Northern Wild Sheep and Goat Council* 2:18-28.

- Rodgers, A. R., A. P. Carr, H. L. Beyer, L. Smith, and J. G. Kie. 2007. HRT: home range tools for ArcGIS. Version 1.1. Ontario Ministry of Natural Resources, Centre for Northern Forest Ecosystem Research., Thunder Bay, Ontario, Canada.
- Rominger, E. M., H. A. Whitlaw, D. L. Weybright, W. C. Dunn, and W. B. Ballard. 2004. The influence of mountain lion predation on bighorn sheep translocations. *Journal of Wildlife Management* 68:993-999.
- Roos, M. D. 1992. The hydrology of the 1987-1992 California drought. State of California, Resources Agency, Department of Water Resources, Division of Flood Management, Sacramento, California, USA.
- Ross, P. I., M. G. Jalkotzy, and M. Festa-Bianchet. 1997. Cougar predation on bighorn sheep in southwestern Alberta during winter. *Canadian Journal of Zoology* 75:771-775.
- SAS Institute Inc. 2011. SAS/STAT® 9.3 User's Guide. SAS Institute Inc., Cary, North Carolina, USA.
- Schaeffer, R. J., S. G. Torres, and V. C. Bleich. 2000. Survivorship and cause-specific mortality in sympatric populations of mountain sheep and mule deer. *California Fish and Game* 86:127-135.
- 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.
- Sesnie, S. E., B. G. Dickson, S. S. Rosenstock, and J. M. Rundall. 2012. A comparison of Landsat TM and MODIS vegetation indices for estimating forage phenology in

- desert bighorn sheep (*Ovis canadensis nelsoni*) habitat in the Sonoran Desert, USA. *International Journal of Remote Sensing*, 33:276-286.
- Sikes, R. S., W. L. Gannon, and the Animal Care and Use Committee of the American Society of Mammalogists. 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. *Journal of Mammalogy* 92:235-253.
- Stevens, D. R., and N. J. Goodson. 1993. Assessing effects of removals for transplanting on a high-elevation bighorn sheep population. *Conservation Biology* 7:908-915.
- Stockwell, C. A., G. C. Bateman, and J. Berger. 1991. Conflicts in national parks: a case study of helicopters and bighorn sheep time budgets at the Grand Canyon. *Biological Conservation* 56:317-328.
- Storer, T. I., and R. L. Usinger. 1968. *Sierra Nevada natural history*. University of California Press, Berkeley, California, USA.
- Torres, S. G., T. M. Mansfield, J. E. Foley, T. Lupo, and A. Brinkhaus. 1996. Mountain lion and human activity in California: testing speculations. *Wildlife Society Bulletin* 24:451-460.
- U.S. Fish and Wildlife Service. 2008. *Recovery plan for the Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*)*. U.S. Fish and Wildlife Service, Portland, Oregon, USA.
- Villepique, J. T., V. C. Bleich, R. A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS collar error: a critical evaluation of Televilt POSREC-science™ collars, and a method for screening location data. *California Fish and Game* 94:155-168.

- Villepique, J. T., B. M. Pierce, V. C. Bleich, and R. T. Bowyer. 2011. Diet of cougars (*Puma concolor*) following a decline in a population of mule deer (*Odocoileus hemionus*): lack of evidence for switching prey. *Southwestern Naturalist* 56:187-192.
- Weber, K. T., M. Burcham, and C. L. Marcum. 2001. Assessing independence of animal locations with association matrices. *Journal of Range Management* 54:21-24.
- Wehausen, J. D. 1980. Sierra Nevada bighorn sheep: history and population ecology. Ph.D. Dissertation, University of Michigan, Ann Arbor, Michigan, USA.
- Wehausen, J. D. 1992. The role of precipitation and temperature in the winter range diet quality of mountain sheep of the Mount Baxter herd, Sierra Nevada. *Biennial Symposium of the North American Wild Sheep and Goat Council* 8:279-292.
- Wehausen, J. 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.
- Whiting, J. C., R. T. Bowyer, J. T. Flinders, V. C. Bleich, and J. G. Kie. 2010. Sexual segregation and use of water by bighorn sheep: implications for conservation. *Animal Conservation* 13:541-548.

Table 1. Hypotheses and general predictions regarding the influence of direct and indirect predation risk, forage availability, and tradeoff of forage at low versus high elevation on habitat selection relationship (+ or -), where relevant, for female and male Sierra Nevada bighorn sheep in the Sierra Nevada, California, USA, 2002–2007.

Hypothesis and corollaries	Direction	
I. Habitat selection influenced by risk of predation		
A) Direct predation risk; surfaces generated from probability density functions of		
Active mountain lions	(-)	(+)
Locations where bighorn sheep were killed and cached by mountain lions	(-)	(+)
B) Indirect (habitat-mediated) predation risk		
Elevation	(+)	(-)
Slope	(+)	(-)
Terrain ruggedness (all radii)	(+)	(-)
Convexity at location (15–30 m radius)	(+)	(-)
Convexity within flight distance (100–150 m radius)	(-)	n/a
Rock cover	(+)	(-)
Tree cover	(-)	(+)
II. Habitat selection influenced by forage availability		
Snow cover	(-)	(+)
Solar radiation	(+)	(-)
Vegetation index	(+)	(-)
III. Tradeoff of forage vs. risk of predation reduced during drought		
NDVI low elevation – NDVI high elevation, above average annual precipitation	(+)	n/a
NDVI low elevation – NDVI high elevation, below average annual precipitation	(-)	n/a

Table 2. Model-averaged parameter estimates, 95% confidence intervals (CI), and Akaike importance weights (AIW) for predictor variables used to model RSF for female and male Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007. Asterisks adjacent to parameter estimates indicate 95% CIs do not overlap zero.

Variable	Female				Male			
	Estimate	Lower CI	Upper CI	AIW	Estimate	Lower CI	Upper CI	AIW
CVX15	0.18	-3.4×10^{-2}	0.40	0.76	—	—	—	—
CVX100	—	—	—	—	-1.1×10^{-2}	-3.4×10^{-2}	1.3×10^{-2}	0.08
CVX150	-3.0×10^{-2}	-8.5×10^{-2}	2.5×10^{-2}	0.29	—	—	—	—
LNRISK	1.2×10^{-2} *	9.4×10^{-3}	1.4×10^{-2}	1.00	2.3×10^{-2} *	2.0×10^{-2}	2.7×10^{-2}	1.00
NDSI	-1.03*	-1.39	-0.67	1.00	—	—	—	—
PRR	0.17*	0.15	0.18	1.00	0.18*	0.15	0.21	1.00
ROCK	-0.12	-0.33	9.4×10^{-2}	0.35	-0.35	-0.80	0.11	0.63
RUG20	—	—	—	—	8.4×10^{-2}	-7.3×10^{-3}	2.4×10^{-2}	0.27
RUG30	-1.3×10^{-3}	-4.4×10^{-3}	1.8×10^{-3}	0.09	—	—	—	—
RUG100	—	—	—	—	6.1×10^{-2} *	3.1×10^{-2}	9.2×10^{-2}	1.00
RUG150	9.4×10^{-2} *	7.6×10^{-2}	0.11	1.00	—	—	—	—
SLOPE	2.6×10^{-2} *	2.1×10^{-2}	3.2×10^{-2}	1.00	3.4×10^{-2} *	2.6×10^{-2}	4.2×10^{-2}	1.00
TRESH	—	—	—	—	-0.64*	-0.94	-0.33	0.97

Notes: Variables in RSF models for winter habitat selection by bighorn sheep included;

convexity over radii of 15 m (CVX15), 100 m (CVX100), 150 m (CVX150), risk surface from locations of active mountain lions (LNRISK), normalized difference snow index (NDSI), potential relative radiation (PRR), rock cover (ROCK), terrain ruggedness over radii of 20 m (RUG20), 30 m (RUG30), 100 m (RUG100), and 150 m (RUG150), slope (degrees; SLOPE), and tree-shrub cover (TRESH).

Table 3. Comparison of resource selection models incorporating risk surface from active mountain lions (LNRISK) with models substituting the correlated predictor elevation (ELEV), for female and male Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007. Substituted variables denoted by bold type.

Model	AIC _c	ΔAIC _c
Female		
CVX15 CVX150 LNRISK NDSI PRR ROCK RUG30 RUG150 SLOPE	7147.0	0.0
CVX15 CVX150 ELEV NDSI PRR ROCK RUG30 RUG150 SLOPE	7220.7	73.7
Male		
CVX100 LNRISK PRR ROCK RUG20 RUG100 SLOPE TRESH	3296.9	0.0
CVX100 ELEV PRR ROCK RUG20 RUG100 SLOPE TRESH	3421.0	124.1

Notes: Variables in RSF models for winter habitat selection by bighorn sheep included; convexity over radii of 15 m (CVX15), 100 m (CVX100), 150 m (CVX150), risk surface from locations of active mountain lions (LNRISK), normalized difference snow index (NDSI), potential relative radiation (PRR), rock cover (ROCK), terrain ruggedness over radii of 20 m (RUG20), 30 m (RUG30), 100 m (RUG100), and 150 m (RUG150), slope (degrees; SLOPE), and tree-shrub cover (TRESH).

Table 4. Cross-validation results for resource-selection functions for female and male Sierra Nevada bighorn sheep, 2002–2007, indicating slope, coefficient of determination (r^2), and Spearman rank correlation (r_s), Sierra Nevada, California, USA, 2002–2007.

Model	Slope	r^2	r_s
Female	0.19	0.95	0.96
Male	0.05	0.81	0.92

Table A1. Description of candidate variables used to model resource selection by Sierra Nevada bighorn sheep and descriptive statistics for 18,240 random locations, Sierra Nevada, California, USA, 2002–2007.

Variable	Description	Mean	SD	Min.	Max
Continuous variables					
KLRISK	Risk surface, locations bighorn sheep kills	33.66	26.46	1.00	99.00
LNRISK	Risk surface, locations active mountain lions	28.83	26.86	1.00	99.00
NDSI	Normalized difference snow index	-2.46×10^{-2}	0.33	-0.67	0.90
NDVI	Normalized difference vegetation index	-0.15	0.14	-0.44	0.59
ELEV	Elevation in meters	2.47×10^3	600.59	1.29×10^3	4.01×10^3
SLOPE	Slope in degrees	33.33	14.31	0.00	80.47
PRR	Potential Relative Radiation	1.17×10^3	532.86	0.00	1.98×10^3
Terrain ruggedness (over specified radius)					
RUG15	15 m	230.40	195.47	0.00	2.70×10^3
RUG20	20 m	411.49	267.63	0.00	3.39×10^3
RUG30	30 m	561.58	309.56	0.00	2.68×10^3
RUG100	100 m	9.93×10^2	390.77	86.63	3.77×10^3
RUG150	150 m	1.14×10^3	404.37	144.56	3.44×10^3
Binary variables (frequency)					
ROCK	Classified from NAIP 2009 image	325	—	—	—
TRESH	Tree and mixed shrub classification	6.66×10^3	—	—	—
Convexity (over specified radius)					
CVX15	15 m	1.69×10^4	—	—	—
CVX20	20 m	1.57×10^4	—	—	—
CVX30	30 m	1.44×10^4	—	—	—
CVX100	100 m	1.10×10^4	—	—	—
CVX150	150 m	1.02×10^4	—	—	—

Table A2. Pearson correlation coefficients for candidate variables at 18,240 random locations used to model resource selection by Sierra Nevada bighorn sheep, Sierra Nevada, California, USA, 2002–2007. Absolute value of $r > 0.60$ denoted by bold type.

Variable	1	2	3	4	5	6	7	8	9	10	11	12	13	14
Biotic and remotely sensed variables														
1. KLRISK	—													
2. LNRISK	0.59	—												
3. NDSI	-0.33	-0.44	—											
4. ROCK	0.09	0.07	-0.04	—										
5. TRESH	-0.08	-0.19	0.09	-0.08	—									
Topographic variables														
6. ELEV	-0.46	-0.73	0.57	-0.04	0.14	—								
7. SLOPE	0.04	-0.14	0.11	0.11	-0.02	0.34	—							
8. PRR	0.02	0.07	-0.15	-0.02	-0.06	-0.06	-0.19	—						
9. RUG20	0.05	-0.04	0.05	0.05	-0.03	0.17	0.37	-0.11	—					
10. RUG100	0.03	-0.11	0.12	0.08	-0.06	0.29	0.55	-0.15	0.49	—				
11. RUG150	0.02	-0.12	0.13	0.08	-0.06	0.29	0.53	-0.14	0.44	0.87	—			
12. CVX15	-0.01	0.03	-0.03	-0.02	0.01	-0.05	-0.20	0.12	-0.18	-0.15	-0.13	—		
13. CVX100	0.00	0.05	-0.05	-0.02	0.02	-0.07	-0.15	0.10	-0.11	-0.18	-0.20	0.17	—	
14. CVX150	0.02	0.04	-0.05	0.00	0.01	-0.03	0.07	0.08	-0.05	-0.11	-0.15	0.11	0.79	—

Notes: Variables in RSF models for winter habitat selection by bighorn sheep included; risk surface from locations of bighorn sheep kills (KLRISK), risk surface from locations of active mountain lions (LNRISK), normalized difference snow index (NDSI), rock cover (ROCK), tree-shrub cover (TRESH), elevation (m; ELEV), slope (degrees; SLOPE), potential relative radiation (PRR), terrain ruggedness over radii of 20 m (RUG20), 30 m (RUG30), 100 m (RUG100), and 150 m (RUG150), convexity within 15 m radius (CVX15), convexity over radii of 15 m (CVX15), 100 m (CVX100), and 150 m (CVX150).

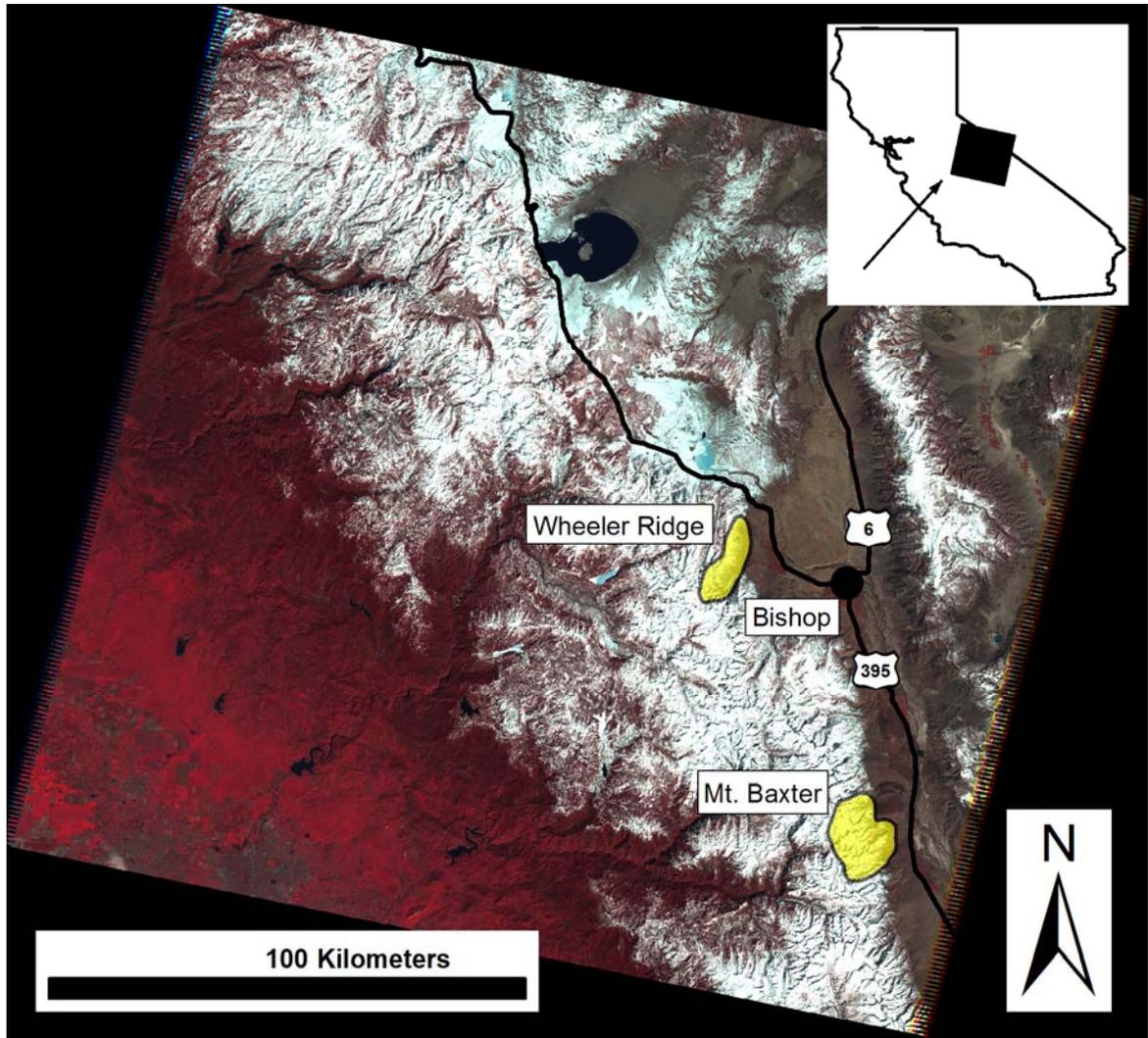


Fig. 1. Landsat scene showing 95% composite home ranges (yellow) for Wheeler Ridge and Mt. Baxter winter ranges of bighorn sheep. Mesic slopes to the west appear red in this false-color image (TM bands 4,3,2) because photosynthetic activity is reflective of infra-red radiation; snow-covered high elevations are visible in the center, with xeric areas visible on the east side, Sierra Nevada, California, USA (Path 42, Row 34, image date 11 March 2005).

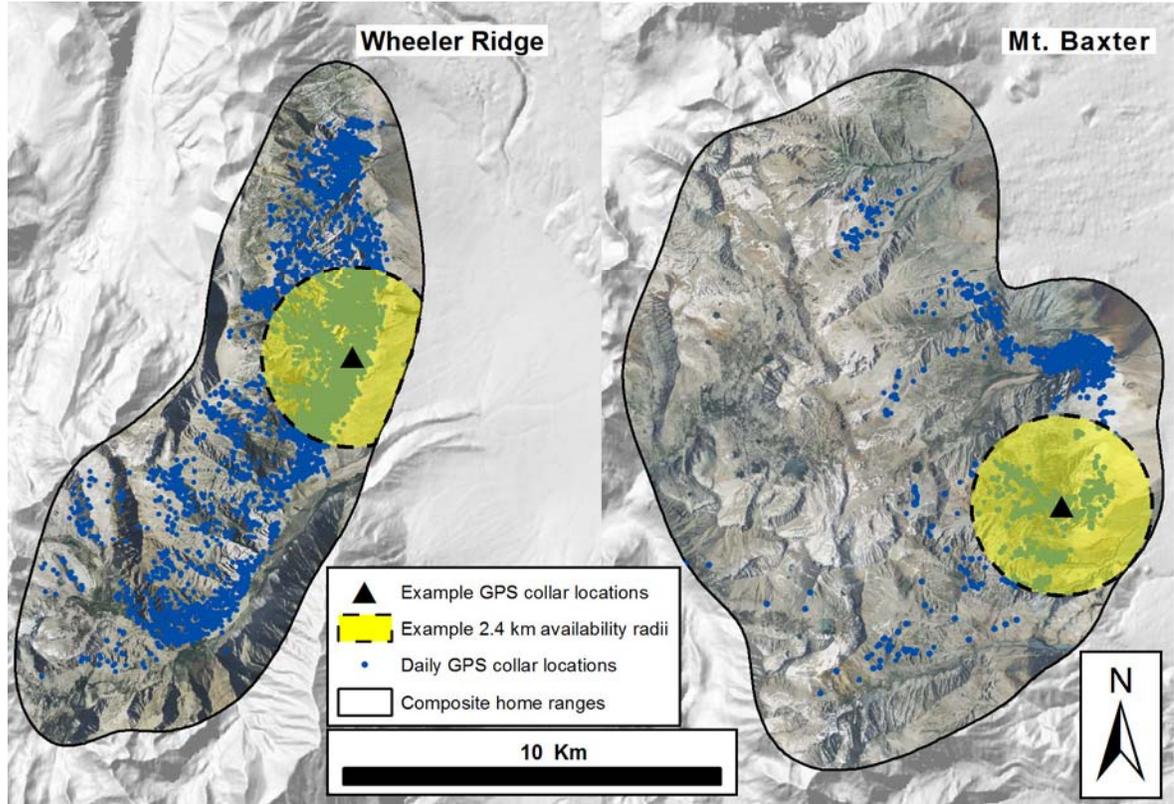


Fig. 2. Example of 2.4-km radius used to define available habitat for each GPS collar location in resource selection function (RSF) for Sierra Nevada Bighorn sheep, California, USA, 2002–2007. Base map within composite home range from National Agricultural Imagery Program (NAIP) 2009 image (1-m scale, true color RGB).

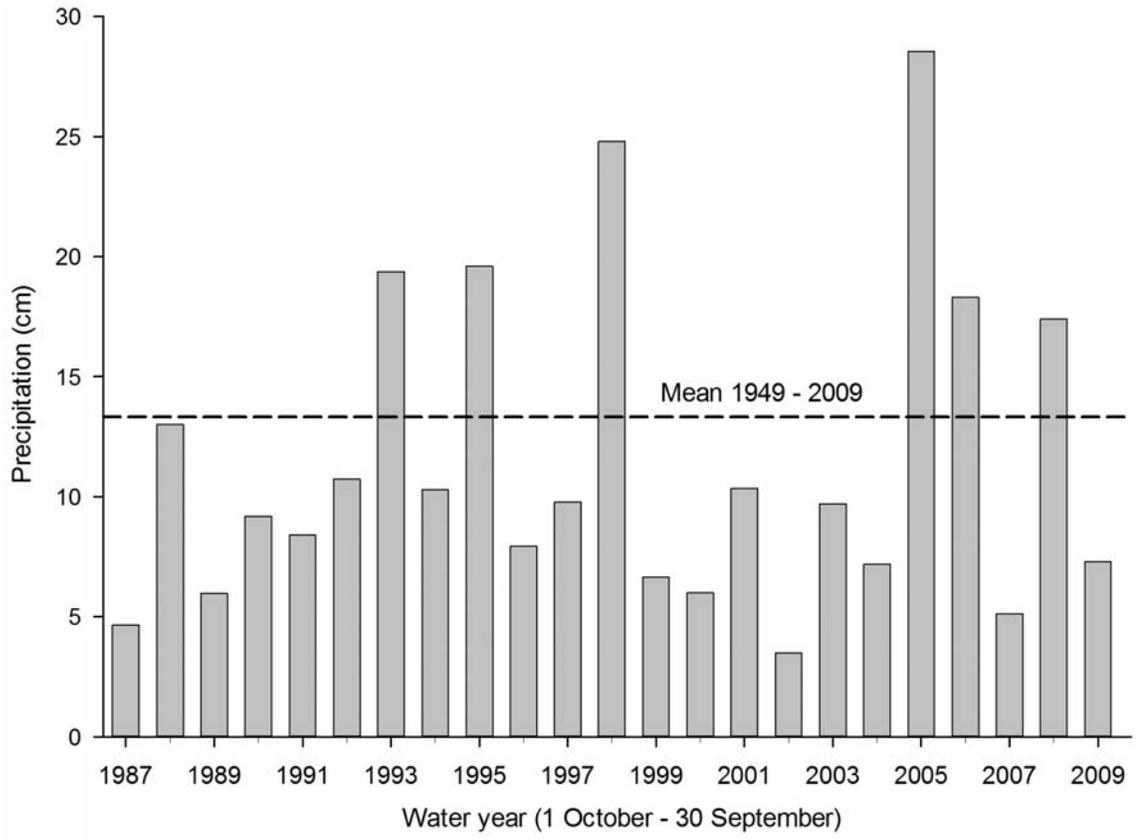


Fig. 4. Annual precipitation and long-term mean (dashed horizontal line), Bishop, California, USA, 1987–2009.

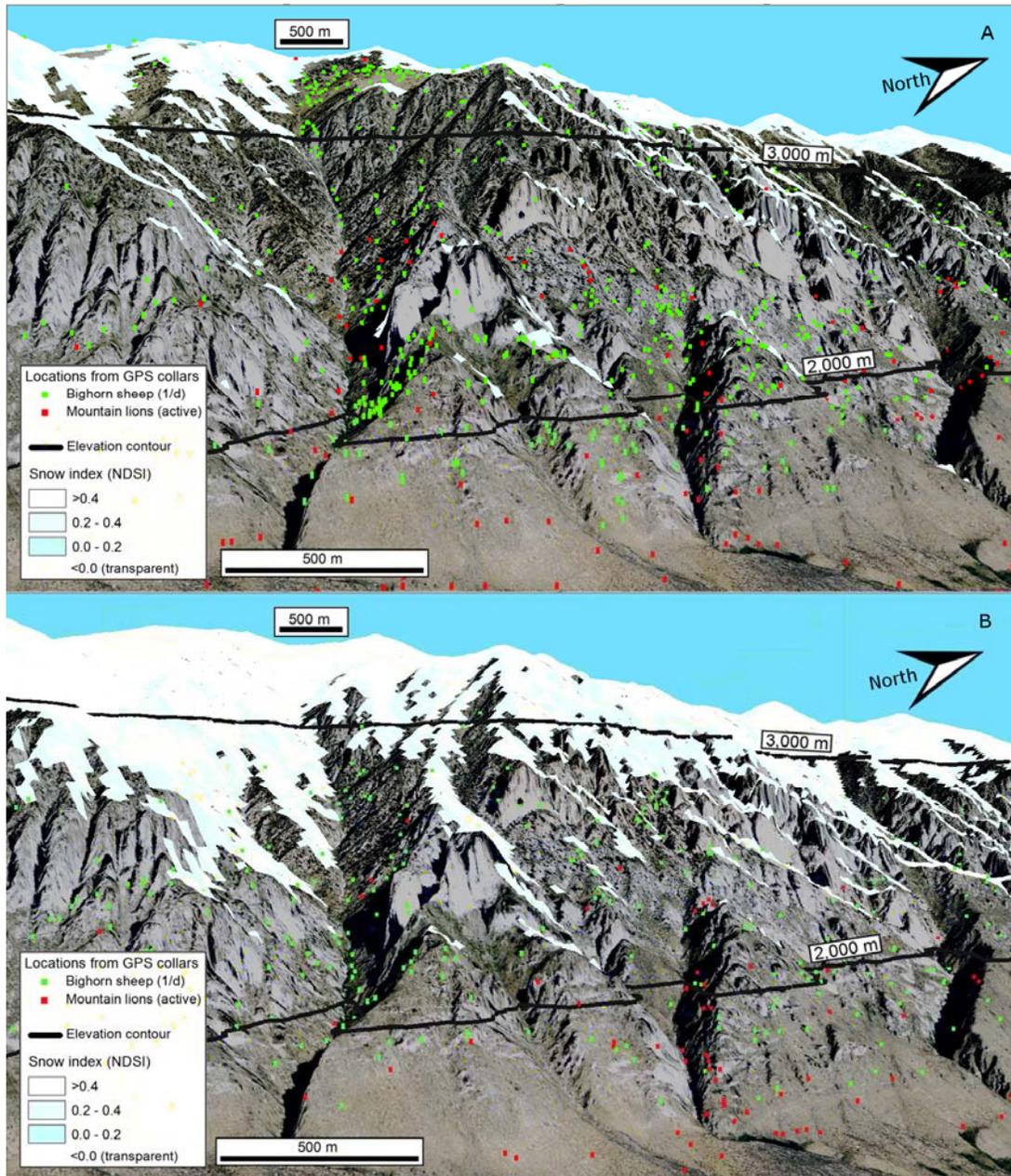


Fig. 5. Representative subset of winter habitat for Sierra Nevada bighorn sheep, illustrated by view of Wheeler Ridge from NAIP 2009 aerial image, indicating high elevation ($>3,000$ m) and low elevation ($<2,000$ m) habitat. Snow cover and locations of bighorn sheep and mountain lions shown for; A) drought years 2002–2004, 2007 ($n = 1,730$ daily locations of bighorn sheep; $n = 1,308$ locations of active mountain lions), with snow cover (NDSI) derived from 12 April 2002 TM image, and B) above-average precipitation years 2005 and 2006, ($n = 957$ daily locations of bighorn sheep; $n = 1,055$ locations of active mountain lions), with snow cover (NDSI) derived from 12 April 2005 TM image. Sierra Nevada, California, USA. Natural color base map is resampled from 1-m native resolution to 10-m pixel size corresponding to horizontal resolution of 10-m DEM used for 3-D visualization. Natural X, Y, and Z dimensions preserved (i.e., no stretch is applied to emphasize relief). NDSI from TM image (Path 42, Row 34).

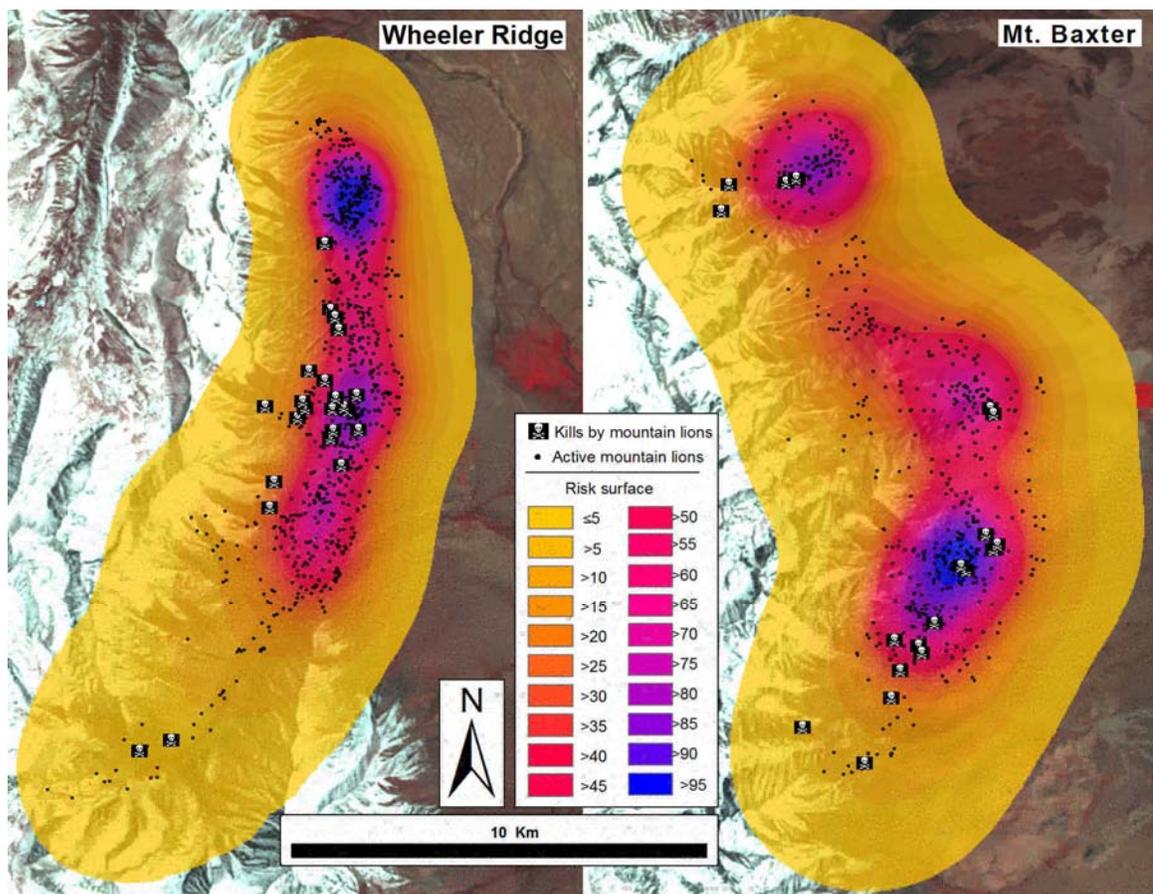


Fig. 6. Risk surface from probability density functions of active mountain lions (LNRISK), expressed as probability density (1–99), overlaid by locations where mountain lions were active, and locations where bighorn sheep were killed or cached by mountain lions, Sierra Nevada, California, USA, 2002–2009. Base map is false-color TM (bands 4,3,2; Path 42, Row 34, image date 11 March 2005).

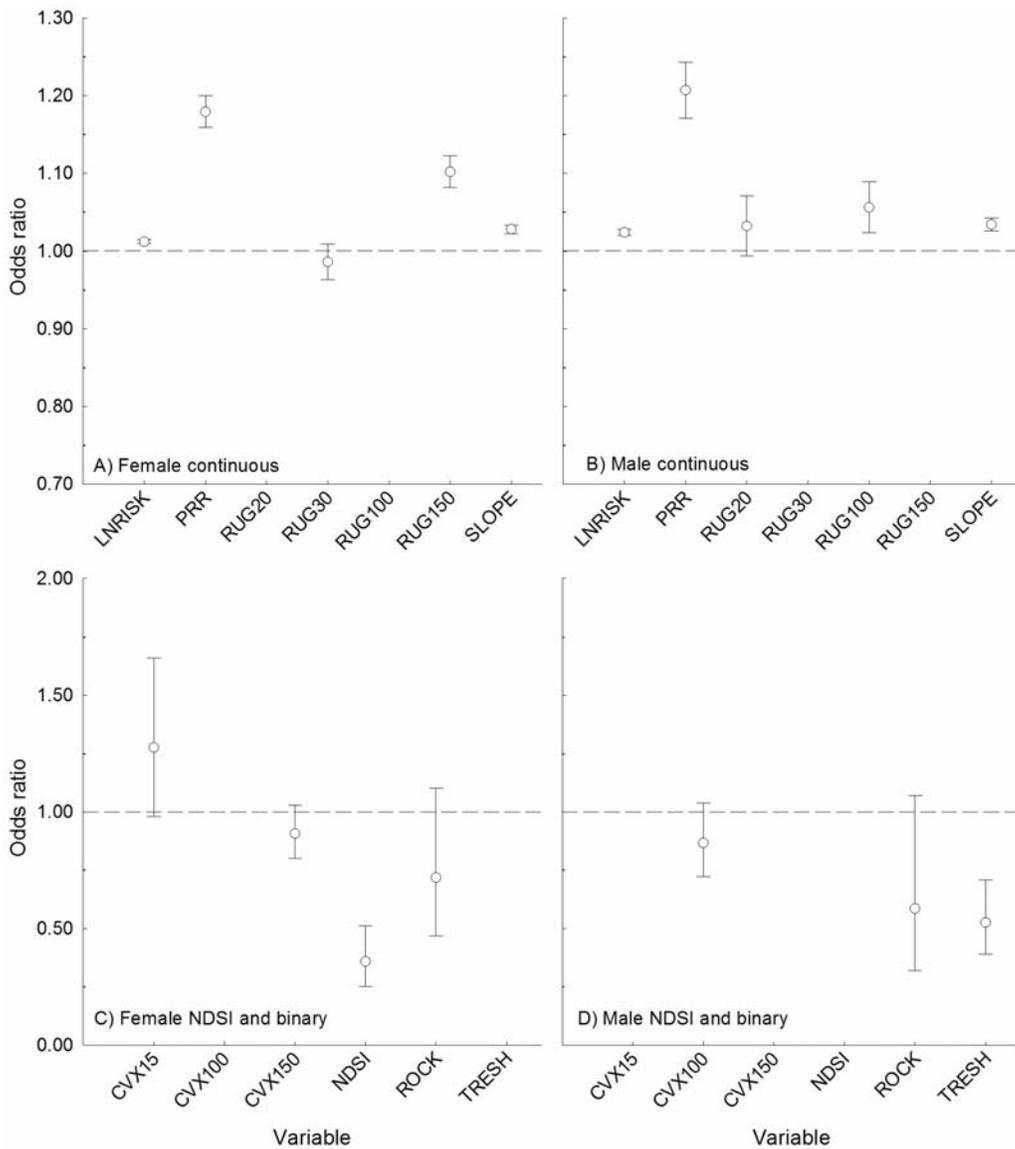


Fig 7. Odds ratios (mean and 95% CI) from resource selection functions (RSFs) for continuous predictor variables used in models of female (A) and male (B) Sierra Nevada bighorn sheep; risk surface from locations of active mountain lions (LNRISK), potential relative radiation (PRR), terrain ruggedness over radii of 20 m (RUG20), 30 m (RUG30), 100 m (RUG100), and 150 m (RUG150), slope (degrees; SLOPE), and odds ratios for normalized difference snow index (NDSI) and binary variables used in models of female (C) and male (D) Sierra Nevada bighorn sheep; convexity over radii of 15 m (CVX15), 100 m (CVX100), 150 m (CVX150), rock cover (ROCK), and tree-shrub cover (TRESH), Sierra Nevada, California, USA, 2002–2007. Odds ratios represent the odds of use (where 1 represents 1:1 chance, i.e., no selection) for every one unit change in continuous predictors; LNRISK, SLOPE, and NDSI, and for each 100 unit change in re-scaled variables PRR, RUG20, RUG30, RUG100, and RUG150. Odds ratios represent the odds of use, given the positive case for each binary predictor, relative to the absence of the binary predictor for, CVX15, CVX100, CVX150, ROCK, TRESH.

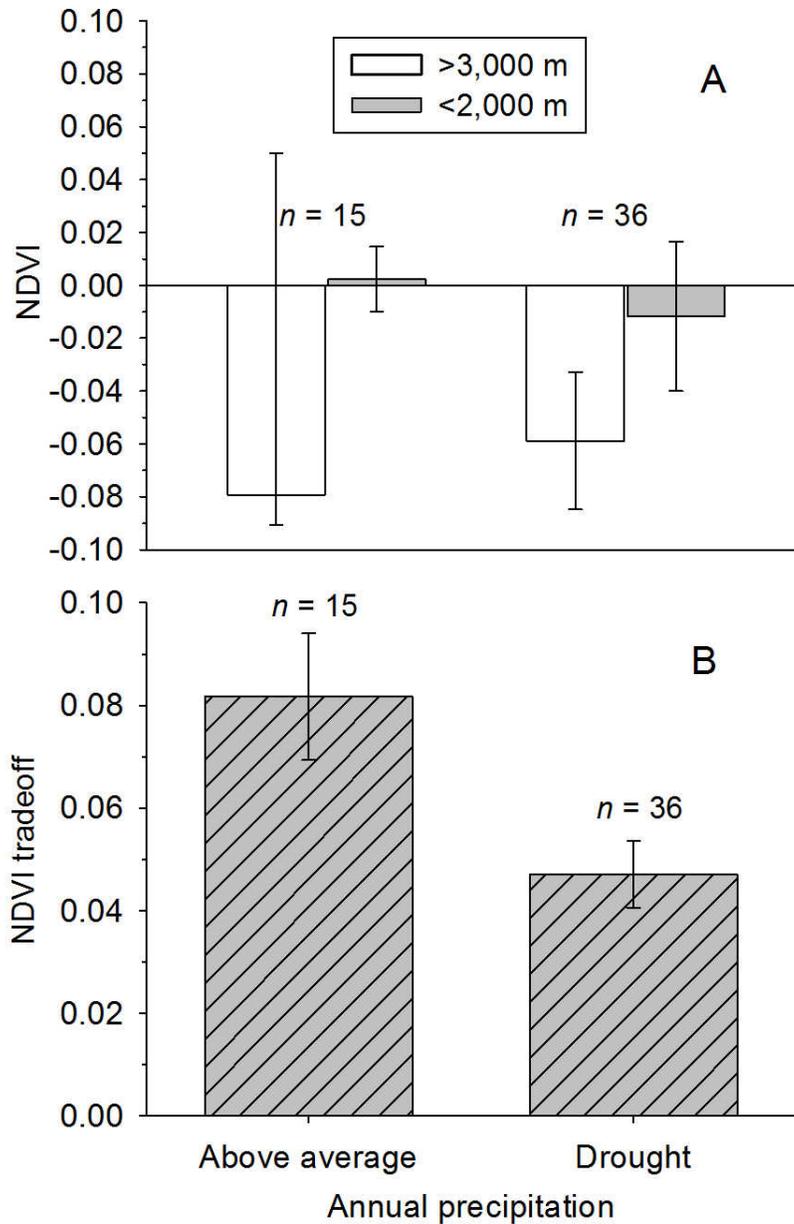


Fig. 8. Comparison of NDVI from Landsat TM in areas used by bighorn sheep in winter (January–April) at high elevations (>3000 m) and low elevations (<2000 m), in above average and below average precipitation years; (A) values of NDVI (mean and 95% CI) at high and low elevations pooled across TM scenes, and (B), tradeoff of vegetation condition at low versus high elevations, measured as difference between NDVI at low elevation and NDVI at high elevation (mean and 95% CI) within each TM scene, Sierra Nevada, California, USA, 1987–1994 and 2002–2009.

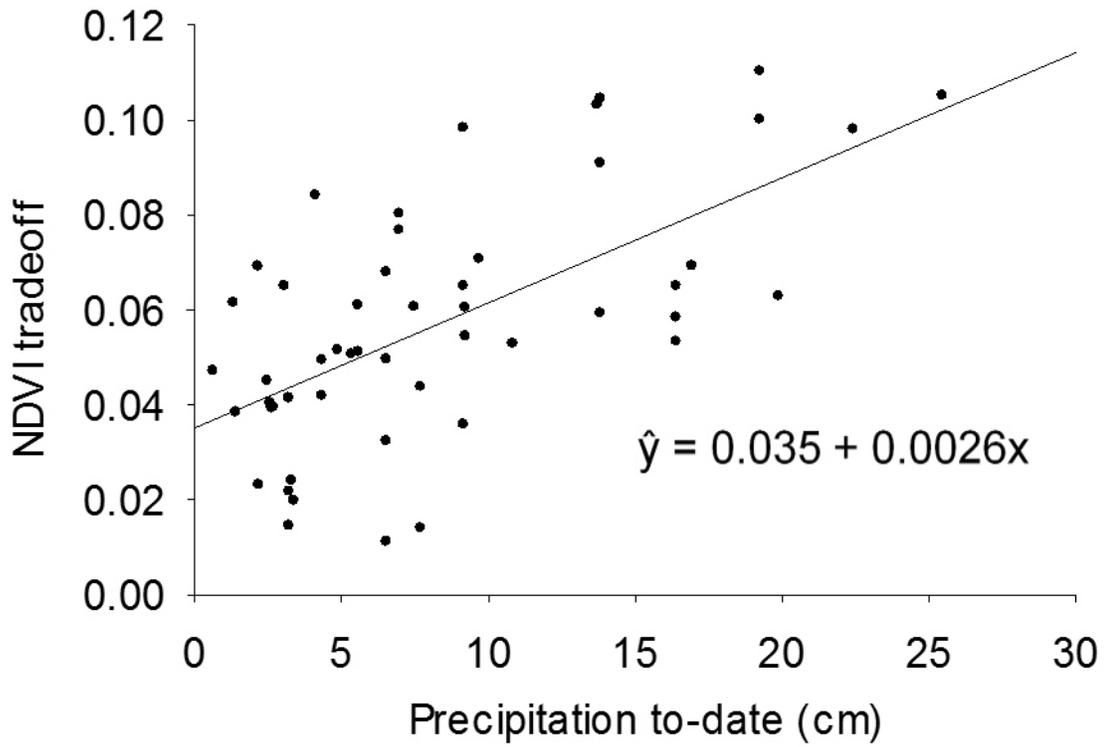


Fig. 9. Relationship between precipitation and NDVI tradeoff ($r^2 = 0.40$; $n = 51$).

Addition of total precipitation of the prior water year (H_2O_{prevYr} ; October 1–September 30) produced a better model fit ($\Delta AIC = 9.6$; $R^2_{adj} = 0.51$; $n = 51$).); $\hat{y} = 0.017 + 0.0030$ x $H_2O_{toDate} + 0.0013$ x H_2O_{prevYr} .

About the BadFix extension

Download URL:

<http://arcscripts.esri.com/details.asp?dbid=14434>

Summary

This extension to ArcView 3.x calculates a few metrics for sequential polyline segments in a polyline shape file and uses them to calculate a predicted probability that a given "movement" resulted from an erroneous GPS fix. BadFix is designed to screen a series of animal movements and detect spurious pseudo-movements (i.e., GPS locations) characterized by an "out-and-back" geometry. We found that such defective GPS locations were frequently generated by Televilt POSREC GPS collars, which may show errors of >1km in some 5% of locations. The BadFix extension was written to perform data salvaging for these collars by identifying clearly erroneous locations. We also found BadFix useful for screening animal movement data from GPS collars that are not defective, as it can flag rare erroneous fixes in large data files, or errors resulting from data transmission (i.e., ARGOS, UHF, or VHF data errors). Argos PTT users may also find use for BadFix in selecting the correct location from the 2 possibles.

Citation

The application of this methodology is presented in a manuscript submitted to the Wildlife Society

Bulletin. If you use BadFix in your work, please cite as:

Villepique, J. T., V. C. Bleich, R.A. Botta, B. M. Pierce, T. R. Stephenson, and R. T. Bowyer. 2008. Evaluating GPS Collar error: A critical evaluation of Televilt POSREC-Science collars and a method for screening location data. California Fish and Game 94:1 55-168.

Dependencies

The BadFix extension works on a polyline theme generated using the "Create Polyline From Point File" option using Animal Movement Extension (Hooge and Eichenlaub 1997) available from:

<http://www.absc.usgs.gov/glba/gistools/>

BadFix requires components of the Distance and Azimuth Tools (v. 1.5-1.7) extension by Jeff Jenness, available from

http://www.jennessent.com/arcview/arcview_extensions.htm and will not run unless this extension active.

How to use

Add the extensions: **BadFix.avx**, and **dist_az_tools.avx** to your EXT32 folder and make them active in your project. Select the Animal Movement polyline theme you wish to screen and click the BadFix button . Click "OK" in the dialog to accept the default logistic model parameters or enter coefficients after generating your own model. The extension will now perform calculations (this could take a few minutes on a slower computer for many 1,000s of records).

In the "Choose probability" dialog box select the threshold for selecting records. For data with no visible problems, choose, 90% or 95%. If you have Televilit Posrec data, I suggest choosing a lower number, even 50% to catch more flawed positions. Click "OK" (Note that this dialog has the

same function as the select query  button. You can also set the screening probability by pushing the select query button and typing ([PredProb]>0.95) -this is the easiest way to look at probability levels of any increment.

This extension selects the segments of an Animal Movement polyline theme that head towards questionable location points so that they appear flagged (i.e., selected) in the view. The user should look to see that selected items are really erroneous (e.g., genuine long movements (e.g., migration) will likely be flagged) and shift-click to unselect a few over-conservatively screened movements, or select a higher predicted probability to avoid flagging good data as bad. In order to weed-out erroneous fixes from the original GPS data one must get back to a point theme. This is possible because records in polyline themes generated with Animal Movement take the attributes of the point they are moving **towards**, thus the flawed point can be identified by these attributes.

One approach to screening using BadFix is to start with a copy of an Animal Movement polyline theme, run BadFix to select suspect "out" movements at the specified probability level, then delete these selected records (or select "switch selection" from the table and copy to a new theme). If the coordinates reside in the screened polyline theme, one can create a new event theme based on this theme's now-screened table. Alternatively, if the original point theme contains a unique record identifier, a tabular join can be used to combine the point them with the polyline theme which contains new fields that quantify the probability of location error.

BadFix adds the following fields to the Animal Movement polyline theme attribute table:

Azimuth -calculated using components of the Distance and Azimuth Tools extension

AngDev -see Zar, Biostatistical Analysis 4th ed., page 604

LgthN_np1 -The mean length of polyline N and N+1

StdDevPoly -The number of standard deviations represented by the length above relative to the 5 previous and subsequent segments

and **PredProb** -The predicted logistic probability that the polyline is the "out" segment of the "out- and-back" pattern created by a bad GPS location.

Provided as-is with no warranty. The scripts are unencrypted so feel free to modify this method and distribute with attribution.

by Jeff Villepique, graduate student, Idaho State University
(villjeff@isu.edu)

APPENDIX II: Avenue source code for BADFIX Extension to ArcView 3.X

```
*** This script calculates the differences in the vectors of sequential
*** azimuths in a table doc. A polyline length field "PLength" is required
*** and is generated using the "AnimalMovement" extension by Hooge &
Eichenlaub,
*** while azimuth requires the "dist_az_tools.avx" by Jeff Jenness,
*** to be active in the project
*** The script prompts for these fields then calculates the following fields in
the table:
*** "AngDev","StdDevPoly","AspectMinDev","Ratem_h","StdDevRate". An
additional field,
*** "BadFix" is added to the table. This empty field is where the user
identifies "good" and
*** "bad" (e.g, with values "1" or "2") locations for use in a logistic
regression in a stats
*** package such as SPSS.
*** The equation used for Angular deviation or "circular standard deviation"
*** is derived from Mardia(1972) and is described as equation 26.22
*** in Zar Biostatistical Analysis 4th ed., page 604
*** by Jeff Villepique
```

```
theView = av.GetActiveDoc
```

```
theTheme= theView.GetActiveThemes.get(0)
```

```
'-----
Test to see that theme is a polyline theme and get fTab if so, otherwise
prompt with error
'-----
if (theTheme.Is(FTheme)) then
  if
(theTheme.GetFTab.GetShapeClass.GetClassName.Contains("Polyline"))
then
  thefTab = theTheme.getfTab
  else MsgBox.Error("Selected theme must be a polyline", "")
  exit
  end
end
'-----
Try setting theme to editable, check that theTheme is editable and
'-----
thefTab.SetEditable(true)
if (thefTab.CanEdit.Not) then
  msgBox.Error(theTheme.GetName+" is not editable, Possible
```

```

permission problem"+
  "Quiting BadFix Screener", "File cannot be edited")
  return nil
end

'-----
' Test if Distance and Azimuth Tools is loaded and run azimuth calculation
'-----
test=Extension.Find("Distance and Azimuth Tools v. 1.6")
If (test=NIL) then
  MsgBox.Error("You must have Jeff Jenness's Distance and Azimuth Tools
extension loaded","BadFix Screener")
  Return(NIL)
End

CalcBearing = av.FindScript("DistanceBearing.CalcBearing")

'-----
' Prompt for user input logistic coefficients or accept defaults
'-----
SearchList = MsgBox.MultilInput("Enter constant and logistic coefficients or
OK to use defaults",
"Calculate logistic scores", {"Enter
constant: _____", "Enter coefficient for LgthN_Np1: _____",
"Enter coefficient for angular deviation:"}, {"-
4.77487", "0.002656", "0.002860"})

constant = SearchList.Get(0).AsNumber
polyLN_NP1beta = SearchList.Get(1).AsNumber
angDevBeta = SearchList.Get(2).AsNumber

'-----
' Initialize var using field from Animal Movement "Create polyline from
point file"
'-----
LengthField = thefTab.findField("Plength")
theShapeField = theFTab.FindField("Shape")

'-----
' set all bits in the selection bitmap to false
'-----
selbitmap = thefTab.getselection
selbitmap.clearall

'-----

```

```

' Add new field to hold Angular Deviation, Std. Deviation of polylength,
' calculated Logistic Probability (using default model), and for user-defined
' good vs. bad (UserDefBad) which may be used in your own logistic
model
'-----
'if (theFTab.FindField("Azimuth") = nil) then

'HasRun = 0 '***** Set flag indicating script has NOT been run before
*****

azimuthField = Field.Make("Azimuth",#FIELD_DECIMAL,5,1)
AngDevField = Field.Make("AngDev",#FIELD_DECIMAL,5,1)
LmeanN_NP1Field = Field.Make("LgthN_NP1",#FIELD_DECIMAL,5,1)
StdDevPolyLField = Field.Make("StdDevPoly",#FIELD_DECIMAL,5,1)
LogRPredProbField = Field.Make("PredProb",#FIELD_DECIMAL,5,1)
UserDefBadField = Field.Make("UserDefBad",#FIELD_DECIMAL,5,1)

theFTab.AddFields ({ Azimuthfield, AngDevField, LmeanN_NP1Field,
StdDevPolyLField, LogRPredProbField, UserDefBadField})

'-----
'Calculate azimuth value borrowed from Jeff Jenness's Distance and
Azimuth Tools extension
'-----
for each aRec in theFTab
  thePolyline = theFTab.ReturnValue(theShapeField, aRec)
  theStart = thePolyline.Along(0)
  theEnd = thePolyline.Along(100)
  theBearing = CalcBearing.Dolt({theStart, theEnd})
  theFTab.SetValue(azimuthfield, aRec, theBearing)
end

'-----
' Initialize vars for custom progress bar
'-----

progress = 0
reckount = theFTab.GetNumRecords

'-----
' Initialize vars for through "n" records through 5th to last
'-----

n=0
for each rec in 0..(reckount - 7) 'Note this prevents error message at end
of execution

```

```
'-----  
'Set custom progress bar  
'-----
```

```
progress = ((n / (recKount - 7) ) * 100)  
av.SetStatus(progress)  
av.ShowMsg(progress.asString.Trim ++ "percent completed")  
  
'-----
```

```
'The following initializes variables for sequential azimuth calc  
'Note that script is aimed at identifying polyline "N" as erroneous  
'and evaluates azimuth, length, [rate], for N & N=1  
' HOWEVER RATE is NOT INCLUDED IN THIS SIMPLIFIED SCRIPT -  
NOR TOPOGRAPHY BELOW  
'topographic factors (slope, aspect) are chosen from attributes Of  
'N-1 as the previous location is likely to better reflect the  
'terrain where the GPS -actually- was when the erroneous location was  
recorded.  
'-----
```

```
anAzimuth = thefTab.ReturnValueNumber(azimuthfield,n)  
NP1Azimuth = thefTab.ReturnValueNumber(azimuthfield,n+1)  
cosAnAzimuth = anAzimuth.AsRadians.cos  
sinAnAzimuth = anAzimuth.AsRadians.sin  
cosNP1Azimuth = NP1Azimuth.AsRadians.cos  
sinNP1Azimuth = NP1Azimuth.AsRadians.sin  
  
'-----
```

```
'Calculate the intermediate "R" value and Angular deviation value  
'-----
```

```
theSquarR = (((sinAnAzimuth + sinNP1Azimuth)/2) * ((sinAnAzimuth +  
sinNP1Azimuth)/2))+  
(((cosAnAzimuth + cosNP1Azimuth)/2) * ((cosAnAzimuth +  
cosNP1Azimuth)/2))  
theR = theSquarR.Sqrt  
theAngDev = (-4.60517*theR.Log(10)).Sqrt *(57.29578)  
  
'-----
```

```
'The following initializes variables for std. dev polylength.  
'-----
```

```
aPLength = thefTab.ReturnValueNumber(Lengthfield,n)  
N_1PLength = thefTab.ReturnValueNumber(Lengthfield,n-1)  
N_2PLength = thefTab.ReturnValueNumber(Lengthfield,n-2)  
N_3PLength = thefTab.ReturnValueNumber(Lengthfield,n-3)  
N_4PLength = thefTab.ReturnValueNumber(Lengthfield,n-4)  
N_5PLength = thefTab.ReturnValueNumber(Lengthfield,n-5)
```

```

NP1PLength = thefTab.ReturnValueNumber(Lengthfield,n+1)
NP2PLength = thefTab.ReturnValueNumber(Lengthfield,n+2)
NP3PLength = thefTab.ReturnValueNumber(Lengthfield,n+3)
NP4PLength = thefTab.ReturnValueNumber(Lengthfield,n+4)
NP5PLength = thefTab.ReturnValueNumber(Lengthfield,n+5)
NP6PLength = thefTab.ReturnValueNumber(Lengthfield,n+6)
thePLengths =
{N_1PLength,N_2PLength,N_3PLength,N_4PLength,N_5PLength,NP2Ple
ngth,NP3PLength,NP4PLength,NP5PLength,NP6PLength}
theCount = thePLengths.count
polyLmeanN_NP1 = (aPLength + NP1PLength)/2

```

```

'-----
'The following calculates stats for std. dev polylength.
'-----

```

```

meanPLength =
(N_1PLength+N_2PLength+N_3PLength+N_4PLength+N_5PLength+NP2Ple
ngth+NP3PLength+NP4PLength+NP5PLength+NP6PLength)/theCount
theSumSquar = (( N_1PLength - meanPLength ) * ( N_1PLength -
meanPLength )) + (( N_2PLength - meanPLength ) * ( N_2PLength -
meanPLength )) +
(( N_3PLength - meanPLength ) * ( N_3PLength - meanPLength )) +
((N_4PLength - meanPLength ) * ( N_4PLength - meanPLength )) +
(( N_5PLength - meanPLength ) * ( N_5PLength - meanPLength )) + ((
NP2PLength - meanPLength ) * ( NP2PLength - meanPLength )) +
((NP3PLength- meanPLength ) * ( NP3PLength - meanPLength )) +
((NP4PLength - meanPLength ) * ( NP4PLength - meanPLength )) +
((NP5PLength - meanPLength ) * ( NP5PLength - meanPLength )) +
((NP6PLength - meanPLength ) * ( NP6PLength - meanPLength ))
theVariance = (theSumSquar)/(theCount-1)
theStdDev = theVariance.Sqrt
StdDevPlus = (polyLmeanN_NP1 - meanPLength)/theStdDev

```

```

'-----
'The following assigns values for new fields
'-----

```

```

thefTab.SetValue(AngDevField,n,theAngDev)
thefTab.SetValue(StdDevPolyLField,n,StdDevPlus)
thefTab.SetValue(LmeanN_NP1Field,n,polyLmeanN_NP1)

```

```

*****
*****

```

```

'-----
***** Calculate the logistic probability and end the Has run before if
then loop *****

```

```

'-----
theLogProb =
(2.7182818^(constant+(polyLN_NP1beta*polyLmeanN_NP1)+(angDevBeta*theAngDev)))/
(1+(2.7182818^(constant+(polyLN_NP1beta*polyLmeanN_NP1)+(angDevBeta*theAngDev))))

thefTab.SetValue(LogRPredProbField,n,theLogProb)

n=n+1
end 'END FOR EACH

'-----
'The following prompts user for cut-off logistic probability to select records
of likely erroneous fixes.
'-----
ProbsList = {"0.95","0.90","0.85","0.80","0.75","0.70","0.50"}
ProbSelCut = MsgBox.ListAsString(ProbsList,
"Enter logistic probability to retain fixes (95% RETAINS more locations,
50% is most selective and REMOVES more locations)",
"Calculation complete: Choose P cut-off")

theQueryStr = "[PredProb]> " + ProbSelCut
thefTab.Query(theQueryStr, selBitmap, #VTAB_SELTYPE_NEW)

thefTab.UpdateSelection

thefTab.SetEditable(False)

```

APPENDIX III: C++ Source code for distance.c cluster selection program

```
#include <iostream>

using namespace std;

//
// main.cpp
// Distance selector
//
// Created by Aleksandra Andic on 13 July 2011.
// May be freely used and modified with attribution
// <insert paper citation>
//

#include <iostream>
#include "ispis.h"
//#include "distance.h"
//#include "days.h"
//#include "record.h"
#include <iostream>
#include <fstream>
#include <strstream>
#include <string.h>
#include <math.h>
#include <map>
#include <cstdlib>

using namespace std;

int main ()
{
    // writing the note about input data and checking is it ready for processing
```

```

int nA(-1);

nA= ispis(5);

if (nA==3){

    //reading in the data and separating main variables

    map<int,string>m_keyfile;
    map<int,string>m_animalID;
    map<int,int>m_datum;
    map<int,float>m_xcoor;
    map<int,float>m_ycoor;

    cout<<"Please enter exact directory path and name of your datafile (/path/name.ext):";

    string s_inputfile, s_input;

    cin >> s_input;

    // s_input="/Users/aandic/Documents/CodeC++/test/LionExport.txt";
    s_inputfile=s_input;

    char buffer1[2048];
    ifstream ostr1(buffer1, 2048);

    int a;
    a=0;

    ifstream fin(s_inputfile.c_str());
    while (fin.good() )
    {

```

```

fin.getline(buffer1, 2048);

char * pch;
int c, pomoc;
float pom;

c=0;

pch = strtok (buffer1, ",");

while (pch != NULL)
{
    if (c==0){m_keyfild[a]=pch;}
    if (c==1){m_animalID[a]=pch;}

    if (c ==2) {
        pomoc = atoi(pch);
        m_datum[a]=pomoc; }
    if (c ==3)
    {pom = atof(pch);
        m_xcoor[a] = pom;}

    if (c ==4)
    {pom = atof(pch);
        m_ycoor[a] = pom;}

    pch = strtok (NULL, ",");
    c=c+1;
}

a=a+1;
}

```

```

// Starting calculations of reference point distances";

// "Setting the reference data ";
int i_max_clusterdistance, i_max_unit,i_max_record;
i_max_clusterdistance=distance(5);
i_max_unit=days(6);
i_max_record=record(i_max_unit);
// counting the different animals

//map cannot be transfered as a variable to int subroutine?
int b=0,c=0,d=0,e=0;
map<int,string>m_differentanimals;
m_differentanimals[0]=m_animalID[0];

cout<<"starting sorting animals"<<endl;
cout<<"animals in dataset:"<<endl;
while (b<a-1){
    cout<<b<<m_animalID[b]<<endl;

    if(m_animalID[b] != m_animalID[b+1]){
        c=0;
        d=0;
        while(c <b){
            if(m_animalID[b+1]==m_differentanimals[c]){d=d+1;}
            c=c+1.;
        }
        if (d==0){
            m_differentanimals[e]=m_animalID[b+1];
            cout<<m_differentanimals[e]<<" " <<endl;
            e=e+1;
        }
    }
    b=b+1;
}

```

```

}

cout<<" "<<endl;

//separating animals by their ID and comparing the data in those separations.

cout<<"Establishing minimum and maximum of given time"<<endl;

int i_max_date=0, i_min_date;

b=0;
while (b<a){
    if(i_max_date<m_datum[b]){i_max_date=m_datum[b];}
    b=b+1;
}

cout<<"maximum time is: "<<i_max_date<<endl;

b=0;
i_min_date=i_max_date;
while (b<a){if (m_datum[b] >0){
    if (i_min_date > m_datum[b]){i_min_date=m_datum[b];}}
    b=b+1;
}

cout<<"minimum time is: "<<i_min_date<<endl;

int i_date,f=0,i_date_kr,g=0;
double d_ref_distance,pom,d_calc_distance,d_dif_distance;
i_date=i_min_date;

cout<<"starting cluster determination"<<endl;

```

```

cout<<"Input a path and a name of the result file:"<<endl;

string s_out,s_outfile;

cin >>s_out;

//s_out="/Users/aandic/Documents/CodeC++/test/clusters.txt"

s_outfile=s_out;

ofstream myfile (s_outfile.c_str());

if (myfile.is_open())

{

while(i_date<i_max_date){

    i_date_kr=i_date+i_max_unit-1;

    cout<<"Processing time interval: "<<i_date<<" - "<<i_date_kr<<endl;

    f=0;

while (f<e){

    cout<<"Processing animal: "<<m_differentanimals[f]<<endl;

    b=0;

while(b<a){

        if(m_differentanimals[f]==m_animalID[b]){

            if(i_date<m_datum[b]){

                if(i_date_kr>m_datum[b]){

                    pom=m_xcoor[b]*m_xcoor[b]+m_ycoor[b]*m_ycoor[b];

                    d_ref_distance=sqrt(pom);

                    g=0;

                    while (g<a){

                        if(m_differentanimals[f]==m_animalID[g]){

                            if(i_date<m_datum[g]){

                                if(i_date_kr>m_datum[g]){

                                    pom=m_xcoor[g]*m_xcoor[g]+m_ycoor[g]*m_ycoor[g];

                                    d_calc_distance=sqrt(pom);

                                    d_dif_distance=d_ref_distance-d_calc_distance;

                                    if (d_dif_distance<0){d_dif_distance=d_dif_distance*(-1);}

                                    if (d_dif_distance<i_max_clusterdistance){

```

```

//racunanje distance

cout<<"Cluster condition satisfied!"<<endl;

        cout<<m_keyfild[b]<<" "<<m_animalID[b]<<" "<<m_datum[b]<<" "<<d_dif_distance<<" "<<m_animalID[g]<<" "
"<<m_keyfild[g]<<endl;

//          myfile
<<m_keyfild[b]<<","<<m_animalID[b]<<","<<m_datum[b]<<","<<d_dif_distance<<","<<m_animalID[g]<<","<<m_datum[g]<<","<<m_keyfild[g]

//          }}}
//          }
//          g=g+1;
//          }

//      }
//      }

//      }
//      b=b+1;
//      }
//      f=f+1;
//      }
//      i_date=i_date+1;
//      }

//      }
//      myfile.close();
}
return 0;
}

```