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LIFE ON THE EDGE: RISK OF PREDATION DRIVES SELECTION OF HABITAT AND SURVIVAL OF NEONATES IN ENDANGERED SIERRA NEVADA BIGHORN SHEEP

Shannon Forshee
University of Montana

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LIFE ON THE EDGE: RISK OF PREDATION DRIVES SELECTION OF HABITAT AND SURVIVAL OF NEONATES IN ENDANGERED SIERRA NEVADA BIGHORN SHEEP

By

SHANNON COLLEEN FORSHEE

B.A. Biology, Eckerd College, St. Petersburg, Florida, 2008
B.A. Environmental Studies, Eckerd College, St. Petersburg, Florida, 2008

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Approved by:

Scott Whittenburg, Dean of The Graduate School
Graduate School

Dr. Michael Mitchell, Chair
Montana Cooperative Wildlife Research Unit

Dr. Thomas Stephenson
California Department of Fish and Wildlife

Dr. Mark Hebblewhite
Wildlife Biology Program

Dr. Paul Lukacs
Wildlife Biology Program

Dr. Creagh Breuner
Organismal Biology and Ecology & Evolution

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Living on the edge: risk of predation drives selection of habitat and survival of neonates in endangered Sierra Nevada bighorn sheep

Chairperson: Dr. Michael Mitchell

Long-term viability of endangered populations requires development of effective management strategies that target the population vital rate with the highest potential to influence population trajectories. When adult survival is high and stable, juvenile recruitment is the vital rate with the greatest potential to improve population trajectories. For my thesis I examined how lactating Sierra Nevada Bighorn sheep *(Ovis Canadensis sierra)* balance forage and predation risk during the neonatal period. I first identified resource selection strategies employed by lactating females to promote survival of neonates and then determined the primary factors affecting survival of neonates. I found lactating females selected for habitat that, despite decreased access to high quality forage, reduced the risk of predation by mountain lions. Understanding the availability of high quality neonate rearing habitat is an important consideration in restoring bighorn populations. My predictive resource selection function models will assist managers in identifying habitat that is most likely to meet the lambing needs of lactating bighorn females. I also found that despite the efforts of lactating female to protect neonates from risks of predation, predation was the strongest factor contributing to variable survival of neonates across subpopulations. I determined that neonates become less vulnerable as they age, were most vulnerable if they were born before the peak birth pulse (April) and if lactating females selected habitat farther from the safety of escape terrain. My work is the first to examine factors affecting selection of neonatal habitat by lactating females and survival of neonates within Sierra bighorn sheep populations. My results have elucidated potential management strategies that may inform recovery actions.

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INTRODUCTION AND OVERVIEW

Introduction

Declines of bighorn sheep (*Ovis canadensis*) populations occurred rapidly across North America with European settlement in the 1800s (Valdez and Krausman 1999), and today Sierra Nevada Bighorn sheep (*O. c.sierra;* Sierra bighorn hereafter), are the rarest subspecies of all North American mountain sheep. The history of Sierra bighorn conservation efforts span centuries; beginning in 1878, when hunting of the species was prohibited (U.S Fish and Wildlife Service 2007). By 1979, disease, illegal hunting, and competition from domestic livestock had reduced the population to approximately 300 individuals distributed across a fraction of their historic range (Wehausen and Jones 2014). Despite intensive efforts by California Department of Fish and Wildlife (CDFW), by 1999 fewer than 130 Sierra bighorns were detected within 3 isolated subpopulations, and the species was emergency listed under the Endangered Species Act. In 2007, U.S Fish and Wildlife Service identified several potential factors limiting Sierra bighorn recovery including: limited distribution, inadequate connectivity, low population size, loss of genetic diversity, predation and disease. Research and subsequent management efforts have sought to address these concerns through translocations, predator control, and disease prevention. Despite considerable progress towards recovery, considerable demographic variation across subpopulations continues to threaten species recovery (U.S Fish and Wildlife Service 2007, Johnson et al. 2010, Conner et al. 2018).

When adult survival is high and stable, juvenile recruitment is the vital rate with the greatest potential to improve population trajectories (Gaillard et al. 2000, Raithel et al. 2007). Although estimates of vital rates for Sierra bighorn sheep have varied widely annually and across subpopulations (Johnson et al. 2010), recent survival estimates for adult females are relatively high and stable (0.78 – 0.99; Conner et al. 2018). Pregnancy rates are also consistently high (90 – 95%), but observed lamb:female ratios estimated in late summer and overwinter are much lower and more variable (21–86%; Greene et al. 2016). Survival of juveniles captured at 6 months to 1 year old was estimated to be 83% (T. Stephenson, California Department of Fish and Wildlife, unpublished data), indicating that mortality of juveniles likely occurs during the neonatal period. Quantifying the factors influencing survival of neonates is important in the development of conservation strategies for improving survival of juveniles and overall population trajectories (Gaillard et al. 1993, Barber-Meyer and Mech 2008).

In the following chapters, I present two main sets of analyses that were intended to reduce the uncertainty surrounding the mechanisms influencing juvenile recruitment and provide managers with recommendations for improving recruitment in Sierra bighorn. In Chapter 1 my objective was to understand how lactating females balance forage acquisition and safety from predators during the early neonatal lambing period. I defined lactating female as any bighorn sheep producing milk for a lamb at-heel. In my second Chapter I sought to test whether predation nutrition, or quality of lambing habitat was the primary factor influencing survival of neonates and to understand how inbreeding depression was affecting survival.

In Chapter 1, I hypothesized that nutrition and predation risk would be key drivers of selection of neonatal lamb rearing habitat by lactating females and evaluated the local adaptations of individual subpopulations to test for a function response to key resources. I quantified the relative probability of selection of neonatal habitat by lactating Sierra bighorn sheep with a used-available resource selection function (RSF; Hosmer and Lemeshow 2000, Manly et al. 2002). I found lactating females selected for habitat that minimized risk of predation by mountain lions on vulnerable neonates, despite decreased access to nutritious forage. I also found variations in resource selection between subpopulations could generally be explained by differences in resource availability. Managers of Sierra Nevada bighorn sheep can use my spatial RSF maps to evaluate the suitability of neonatal lamb rearing habitat within potential reintroduction sites. Recolonization into historic ranges and interconnectivity between subpopulations is a key component in species recovery and ensuring long-term viability of fragmented subpopulations.

In Chapter 2, I evaluated competing hypotheses to test whether quality of habitat selected by lactating females, nutrition (female body condition), predation risk, or habitat quality selected by lactating females had the greatest effect on survival of Sierra bighorn sheep neonates (0–90 days) and if inbreeding depression was negatively influencing survival. I tested these hypotheses using nest-survival analysis (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer and Thompson 2007). I found that predation risk was the primary driver of survival for neonates. Vulnerability of neonates to predators was highest for early-born neonates, neonates farther from escape terrain, and decreased as neonates age. Although managers may not be able to directly mitigate mortality of neonates, managers may be able to entice lactating females to remain closer to escape terrain by conducting prescribed burns to improving nutritious forage near escape terrain (Greene et al. 2012). Overall, my work reveals that predation risk is a strong force governing selection of habitat by lactating females and survival for Sierra Bighorn sheep neonates. Management practices that can improve survival of neonates have the potential to improve population growth within subpopulations where adult survival is high and recruitment is low, which may have long-term effects on the recovery of Sierra Bighorn sheep.

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CHAPTER 1

PREDATOR AVOIDANCE STRATEGIES DRIVE SELECTION OF NEONATAL LAMBING HABITAT BY LACTATING SIERRA NEVADA BIGHORN SHEEP

ABSTRACT

Predation risk has shaped the selection of habitat by ungulates, leading to trade-offs in selection of habitat between acquiring quality forage and minimizing risk of predation. These compromises are thought to be strongest for lactating ungulates because of the high nutritional demands of lactation and increased vulnerability of juveniles to predators. I examined selection of habitat by federally endangered Sierra Nevada bighorn sheep (*Ovis canadensis sierrae)* during the neonatal period. I hypothesized that lactating females should select for habitat that minimizes risk of predation. As predicted, I found lactating females strongly selected for habitat near escape terrain with high visibility and avoided habitat where the relative probability of encountering mountain lions (*Felis concolor*) was higher. Despite decreased access to high quality forage, my results show that females selected habitat that reduced the risk of predation on neonates. Understanding the availability of high quality neonate rearing habitat is an important consideration in restoring bighorn populations. Our models will assist managers in identifying habitat that is most likely to meet the lambing needs of lactating bighorn sheep and facilitate recovery of Sierra Nevada bighorn.

KEY WORDS: Sierra Nevada bighorn sheep, Mountain lion, predation, nutrition, lamb rearing habitat, resource selection function

INTRODUCTION

For prey species, balancing selection of habitat that maximizes acquisition of high quality forage against the constraints from risk of predation results in critical trade-offs between safe and productive foraging areas (Festa-Bianchet 1988, Lima and Dill 1990, Hamel and Côté 2007). Habitat can be defined as the biotic and abiotic resources that determine the presence, survival and reproductive fitness of a species (Sinclair et al. 2006). When a positive correlation exists between predation risk and forage, ungulates must select from a continuum of low forage and low risk of predation areas to high forage and high risk areas (Bowyer et al. 1998, Mitchell and Lima 2002, Hebblewhite and Merrill 2009). Risk of predation is strongly related to selection of habitat and spatial distribution of predators. (Lima and Dill 1990, Hebblewhite et al. 2005). Prey can minimize predation risk through selection of habitat that reduces the likelihood of encountering predators, increases the likelihood of detection and evasion of predators, or minimizes the odds of predator success (Risenhoover and Bailey 1985, Hebblewhite and Merrill 2009, DeMars and Boutin 2018). Such behavioral adaptations often result in decreased food intake, increased stress levels, and can negatively affect survival and reproductive success of prey (Brown and Kolter 2004, Fortin et al. 2005, Thaker et al. 2011). Balancing nutrition and predation risk is most crucial for lactating ungulates in the first month post-partum, as energetic requirements for females increase between 65–215% (Oftedal 1985, Parker et al. 2009) and neonatal offspring are most vulnerable to predation (Gaillard et al. 1998, Hamel and Côté 2007, Smith et al. 2014). Selection of habitat by lactating females can have direct consequences on fitness of females as well as survival of offspring (Berger 1991, Rachlow and Bowyer 1994, Bangs et al. 2005).

Natural selection should favor female ungulates that employ strategies that promote survival of offspring (Festa-Bianchet 1988). Birthing seasons for alpine ungulates are synchronous with the narrow window of favorable climactic conditions and phenology of vegetation. In addition to providing adequate nourishment for growth and development of offspring during this time, maternal ungulates must also replenish their own body reserves in preparation for over-winter survival when nutritional intake is expected to be limited (Bunnell 1982, Rachlow and Boywer 1994, Parker et al. 2009). Neonatal offspring are highly vulnerable to predation (Gaillard et al. 1998, Laundre 2008). Migration of alpine ungulates to higher elevations in spring is expected to reduce the likelihood of encountering predators at larger spatial scales (Hebblewhite and Merrill 2009), yet this strategy can result in reduced access to forage biomass (Nicholson et al. 1997, Spitz et al. In Press). Proximity to rugged escape terrain and use of open terrain with high visibility has been consistently noted as strategies for reducing predation risk at smaller spatial scales, but these areas generally provide limited access to forage (Geist 1971, Festa-Bianchet 1988, Berger 1991, Wehausen 1996, Hamel and Côté 2007). Lactating females must make trade-offs between acquiring high quality forage and avoidance of predation risk. The consequences of these trade-offs are challenging to predict, yet for threatened or endangered ungulate populations, understanding the factors driving these behavioral strategies is important for guiding management decisions.

Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* Sierra bighorn sheep hereafter) are a federally endangered subspecies of bighorn sheep endemic to the Sierra Nevada of California (U.S Fish and Wildlife Service 2007, Wehausen and Jones 2014). This metapopulation currently consists of 14 subpopulations distributed along the Sierra Nevada crest. In 2007, U.S Fish and Wildlife Service identified several potential factors limiting Sierra bighorn sheep recovery including: limited distribution, inadequate connectivity between subpopulations, small population size, loss of genetic diversity, predation, and disease. Research and subsequent management efforts have sought to address those concerns through translocations, predator control and disease prevention (Johnson et al. 2010, 2011, 2013, Greene et al. 2012, Clifford et al. 2009, Cahn et al. 2011). Despite considerable progress towards recovery, subpopulations continue to exhibit highly variable and population-specific dynamics (U.S Fish and Wildlife Service 2007, Johnson et al. 2010, Conner et al. 2018). Subpopulations are geographically grouped into metapopulation recovery units: Northern, Central, Southern and Kern (Figure 1).

Long-term viability of naturally fragmented subpopulations can be achieved through inter-population connectivity and recolonization of suitable habitat. Sierra bighorn sheep are philopatric and slow to naturally recolonize, thus recent conservation efforts have focused on reintroductions throughout former ranges and augmentation of smaller subpopulations (Geist 1971, Few et al. 2015). The historical distribution of Sierra bighorn sheep remains poorly understood because the species was nearly extirpated before being listed for protection (Wehausen and Jones 2014). Furthermore, little is known about patterns of habitat selection by lactating females during the early neonatal period. Much of the previous research describing lambing habitat was largely based on observations of lambs, not known birth events, and thus are potentially biased towards areas of greater visibility or habitat used by pairs when lambs are more mobile (Bangs et al. 2005, Barbknecht 2008, Smith et al. 2015). Smith et al. (2015) reported that >80% of documented parturition sites occurred outside of lambing habitat previously delineated through observations. To improve translocation success and ultimately aid in the recovery of Sierra bighorn sheep, it is important to quantify neonatal habitat.

My objective was to evaluate how lactating females balance forage acquisition and safety from predators during the early neonatal lambing period. I first tested for a forage-risk trade-off within each subpopulations spring range. I hypothesized that forage and risk of predation from mountain lions would be positively correlated, and expected that Sierra bighorn females would make trade-offs between safety and forage acquisition. I then hypothesized that lactating females should select for habitat that minimizes risk of predation on vulnerable neonates. Accordingly, I predicted strong avoidance of habitat with high probability of encountering predators, strong selection for habitat with good visibility and proximity to escape terrain. Alternatively, I hypothesized that lactating females should select habitat that maximizes access to high quality nutrition to meet increased nutritional demands of lactation. Thus, I predicted strong selection for habitat where access to forage biomass is greatest. I evaluated the potential for a functional response from females to several key habitat resources and examined local adaptations of individual subpopulations by comparing availability of habitat resources and selection among subpopulations. I hypothesized that variation in availability of quality forage and exposure to predation risk would explain potential differences in selection strength for these resources between subpopulations. Consequently, I predicted subpopulations with decreased availability of forage resources would show increased selection for forage and subpopulations with increased availability of forage would show decreased strength of selection. I also predicted that subpopulations with greater risk of predation (higher risk of encounter or lower proportion of escape terrain) would show greater avoidance of encounter risk and increased selection for proximity to escape terrain.

STUDY AREA

The Sierra Nevada extends 650 km along the Eastern border of California (Hill 1975). Sierra bighorn sheep subpopulations are historically and currently restricted to the most alpine habitat along the Southeast portion of the range (U.S Fish and Wildlife 2007). Subpopulations extend from Lee Vining, California approximately 200 km south near Olancha, California. Elevation along the Eastern front changes abruptly from 1000 m to an average of 3,000 m, with numerous peaks above 4,000 m. Sierra bighorn sheep are considered partially migratory, many individuals spending winters at lower elevations and migrating upwards in spring months (U.S Fish and Wildlife 2007, Spitz et al. In Press). The strong rain shadow effect limits summer (May-September) precipitation east of the Sierra crest, thus most of the annual precipitation falls as snow during winter months (November-April). Granitic and volcanic soil types are nutrient limited and predominant throughout the range (Hill 1975). The xeric vegetation communities are separated by elevation classes, low-elevation (1500–2499 m) includes scrub with mixed grass and forb types; intermediate (2500–3300 m) includes moderate timber cover with sparse forbs and subalpine meadows; high elevations (>3300 m) includes sparse alpine vegetation (Hill 1975). Common fauna includes mule deer (*Odocoileus hemionus*), mountain lion (*Puma concolor),* bobcat *(Lynx rufus),* black bear *(Ursus americanus),* coyote *(Canis latrans),* and golden eagle *(Aquila chrysaetos).* The strong overlap of mule deer populations with low-elevation Sierra bighorn sheep ranges, leads to predator-mediated apparent competition by mountain lions (Johnson et al. 2013). Predation by mountain lions has been a leading cause of adult Sierra bighorn sheep mortality in numerous subpopulations for decades, accounting for approximately 53% of all known mortalities (Johnson et al. 2013, Stephenson et al. 2012, Conner et al. 2018).

METHODS

California Department of Fish and Wildlife crews captured adult female Sierra bighorn sheep across seven subpopulations from 2008 – 2018 by helicopter net-gun and fitted them with global positioning system (GPS) collars (University of Montana IACUC 012–16MMMCWRU–022916, Federal Fish and Wildlife Service Permit No. TE050122–4) as a part of a long-term monitoring effort for recovery. These seven subpopulations are the focus of extensive data collection and represent >85% of the subspecies. Collars were programmed to record >1 location at regular time intervals (2–12 hours). We determined pregnancy using ultrasonography (Stephenson et al. 1998). I fitted a sub-sample of pregnant females with vaginal implant transmitters (VIT) and high fix rate collars (12 fixes/day) during 2016 – 2017 (Bishop et al. 2007). I included 30 days of post-partum GPS locations from resident females each lamb-year to represent the early neonatal lamb rearing period beginning on the date of parturition.

I developed an algorithm for estimating date of parturition based on locations of collared ewes using the adehabitat package (Calenge 2006) in Program R (R Core Team 2018); Appendix A). I analyzed movement patterns pre, during, and post-partum for a sub-sample (n =22) of females with high fix-rate GPS collars and VITs to develop a model that predicted parturition for these females (DeMars et al. 2013, McClintock et al. 2012, 2014, Blackwell et al. 2016). I found that on average, females spent ($\bar{\chi}$ = 26 hours , SE = 4) in a parturition site and remained within an average of ($\bar{\chi}$ =19m , SE= 11) from the site until departing. I tested this model by comparing known parturition sightings to model predictions (n=21). I also tested for false positives (clustered GPS locations due to extended or consecutive use of bedsite) using GPS data from females (n=6) that were not pregnant. I applied this cluster detection algorithm to all sampled females within our study.

I calculated the probability of detecting a lamb known to be present using mark-resight estimation based on the presence of lamb-at-heel for marked females by surveying spring lamb ranges during the early neonatal lambing period (Bonenfant et al. 2005). Because twinning has not been observed in Sierra bighorn and females do not allow non-related offspring to suckle, visual observations reliably indicate lamb presence and absence. I made multiple attempts to confirm the presence of a lamb for each female, and to resight pairs through the early neonatal period. I estimated the probability of sighting and resighting a lamb for each occasion a female was observed post-partum during the early neonatal period.

Selection of Neonatal Habitat

I evaluated the relative probability of selection of neonatal habitat by lactating Sierra bighorn sheep with a used-available resource selection function (RSF) by using the exponential approximation to the inhomogenous poisson point process (Aarts et al. 2012, Lele et al. 2013, McDonald 2013). I used a 99% kernel density estimator (KDE) with 100m buffer (Worton 1989) to delineate spring home range for each subpopulation from all compiled GPS locations from all collared females within each subpopulation from April 1 –July 15th from all years. I sampled available locations within each subpopulation's home range (Johnson 1980, Boyce 2006) using a 4:1 ratio of stratified random available locations to used GPS locations (Benson et al. 2013, Northrup et al. 2013).

Resource variables − I selected vegetative, topographic and biotic explanatory variables to test my hypotheses (Table 1). I included a spatial predation risk variable developed from a mountain lion RSF derived specifically for my study area in spring months (Appendix B).
I built a third-order used-available design RSF based on GPS locations from 28 radiomarked mountain lions within my study area from 2002-2011. I included GPS locations from

crepuscular hours estimate selection of habitat that primarily reflected hunting behaviors, and considered the resulting RSF was correlated with relative probability of encountering a hunting mountain lion (Lima and Dill 1990, Hebblewhite et al. 2005, Hebblewhite and Merrill 2007, 2009; Johnson et al. 2013). I mapped spatial encounter risk at a 30m resolution. I defined escape terrain for Sierra bighorn sheep as slopes > 42°. I examined distance to escape terrain by binning distances into levels of risk; Low: 0–120 m, Med: 121–240 m, and High: < 240 m (Fairbanks et al. 1987, Harris et al. 1995). I included the Normalized Difference Vegetation Index (NDVI) metric to represent relative forage biomass, a proxy for vegetation quality and net primary productivity in open canopied landcover types (Borowik et al. 2013). I obtained composite layers from the MOD13Q1 data product from the moderate-resolution imaging spectroradiometer (MODIS) satellite (Didan 2015). I used 16-day composites of surface reflectance values to calculate NDVI vales from April 1- July15th for the years 2006 – 2017 at the spatial resolution of 250m (Pettorelli et al. 2007, Hamel et al. 2009, Sensi et al. 2012). I processed NDVI data following previously established protocols, excluding locations contaminated by cloud cover (Hamel et al. 2009). I extracted NDVI values from the composite layer that matched the date of use by each female. For available locations, I calculated the median NDVI from the annual time series data-sets for each available cell across the study area (Pettorelli et al. 2007, Hebblewhite et al. 2008, Hebblewhite and Merrill 2009). I included thematic vegetation layers from CalVEG condensed to 4 categories to represent basic vegetation types. I focused on NDVI values within herbaceous and barren vegetation types because they represent grasses and forb species primarily consumed by Sierra bighorn sheep (Wehausen and Hansen 1988, Greene et al. 2012, Borowik et al. 2013). I standardized continuous variables by subtracting each value from the mean of all values across the study area and dividing by the standard deviation so that the magnitude of each variable was comparable across models (Bring 1994). I extracted variables for all GPS locations using digital raster layers at the 30m resolution in Program R (3.1.4) and ArcGIS (10.5.1). I tested the correlation structure between forage and predation risk using 8,000 random locations within subpopulation spring home ranges that were delineated as either barren or herbaceous vegetation types using Pearson correlation coefficients.

Model fitting and selection.− I retained candidate variables that were non-confounded and screened for collinearity using the Pearson correlation coefficient threshold of $|r| \leq 0.6$ (Hosmer and Lemeshow 2000, Wickham 2009). Among collinear-pairs, I retained the variable that had stronger predictive ability (Austin 2002). I built thirteen candidate models to test my hypotheses using a generalized linear mixed-effects modeling (GLMM) framework and a random intercept for individual females and subpopulations to account for unbalanced sample sizes between individually collared females and subpopulations (Skrondal & Rabe-Hesketh 2004, Gilles et al. 2006).

I ranked top models using Bayesian Information Criteria (BIC); models with the lowest BIC were most supported by the data and I considered models with ≤ 2 ΔBIC to be competitive (Schwartz 1978, Hooten and Hobbs 2015). I evaluated overfitting, multicollinearity and improved variable selection for my top candidate models using a regularization multiplier through the least absolute shrinkage and selection operator (LASSO; glmmLasso; Tibshirani 1996, Francais et al. 2017). I considered standardized β-coefficients with confidence intervals that did not overlap 0, and defined coefficients ≤ 0.1 to have weak effects on selection, values $\geq |0.1|$ and ≤ 0.5 moderate, values $\geq |0.5|$ and $\leq |1.0|$ strong, and values $\geq |1.0|$ to have very strong effects (Bring 1994).

Model testing and projection.– I evaluated the predictive capacity of the top performing model by averaging the results from 100 iterations of k-fold cross validation and derived Spearman Rank coefficients (Boyce et al. 2002, Fernandez et al. 2003, Maindonald and Braun 2006). I externally tested the top model using an independent sample of GPS locations from lactating bighorn sheep in 2018 withheld from model building. I multiplied the fixed effect β-coefficients from the top model with corresponding spatial variable raster layers to project the relative probability of selection across the study site. I applied the top model to each subpopulation data set, with a random effect for individual (Manly et al. 2002, Beyer et al. 2010) to evaluate relative differences in selection among subpopulations.

Subpopulation characteristics.− I calculated the proportional availability of resources related to forage (vegetation types) and predation risk (risk of encountering a mountain lion and distance to escape terrain) systematically sampled within each subpopulation's spring home range to evaluate if selection varies as a function of availability (Benson 2013). I ranked level of predation risk based on the percentage of known mortalities from mountain lions occurring within 3 levels of relative predicted probabilities of encounter: Low (12%), Medium (38%), High (>50%). I fit a general linear model using regression analysis to test for a functional response by females to key resources and evaluate differences between subpopulations. I considered the strength of correlation between availability of a resource and selection coefficient as well as the proportion of variation in selection explained by availability.

RESULTS

From 2006- 2017 California Department of Fish and Wildlife collected a total of 34,763 GPS locations from 30 days post-partum across 123 unique female-lamb pairs for model building;

2,286 from 24 pairs in Mt. Warren, 1,529 from 8 pairs in Mt. Gibbs, 2,643 from 11 pairs in Convict Creek, 8,268 from 21 pairs in Wheeler Ridge , 6,148 from 16 pairs in Sawmill Canyon, 7,614 from 18 pairs in Mt. Baxter, and 6,275 from 25 pairs in Mt. Langley. I used 1,280 GPS locations from 14 pairs in 2018 to test model fit. Using mark-resight, I estimated the probability of sighting and resighting a lamb as 0.96 (SE=0.04, n=36 known present lambs) for each occasion a female was observed. I made an average of 3.42 observations per female during the 30 day period, and only included data from females with ≥ 2 observations, thus on average there was <1% chance in missing a lamb.

Selection of Neonatal Habitat

Resource variable− Slope, elevation, NDVI, and predation risk were highly correlated. I retained predation risk as this metric had strong explanatory power for selection of habit by lactating females and incorporated slope, elevation and NDVI in RSF models (Lehman et al. 2002, Austin 2002). I found that forage biomass was positively correlated with risk of predation at randomly available locations throughout the spring Sierra bighorn sheep ranges (r =0 .73, P< 0.001). The correlation was too strong to include predation risk and forage, as estimated by NDVI, within the same model. Thus, I evaluated the trade-offs between forage and predation risk within forage vegetation types. I found that on average herbaceous vegetation had a relatively high risk of encounter ($\bar{\chi}$ = 48%), whereas barren vegetation had relatively low risk ($\bar{\chi}$ = 18%).

Model fitting and selection.− There was low model uncertainty among top candidate models explaining selection of habitat by lactating Sierra bighorn sheep; the top five models included the same six base variables with alternative combinations of additional variables (Table 2). I selected the second ranked model because it was more parsimonious and the additional covariates were uninformative (Arnold 2010). The fixed effects ß-coefficients of the top selection model suggested that during the early neonatal period, lactating Sierra bighorn sheep selected most strongly for habitat within 120m of escape terrain (β=2.30, SE=0.03), followed by habitat within 240m (β=1.15, SE=0.03; Table 3), relative to habitat < 240 m. Females strongly selected for barren vegetation types (β=0.85, SE=0.03), shrubs (β=0.81, SE=0.03), and slightly for herbaceous vegetation (β=0.31 SE=0.04) when predation risk was zero. Females showed strong avoidance of habitat with increasing probabilities of encountering a hunting mountain lion in all vegetation types other than barren (β= -0.64, SE=0.02). Females showed strong selection for barren habitat with increasing predation risk (β= 0.70, SE=0.02; (Figure 2). Selection was weak for increasing values of TPI (β= 0.09, SE=0.003). I found very low individual-level variation in resource selection between individuals (n= 123, SD <0.001), and minimal variation at the subpopulation level (n= 7, SD= 0.101) compared to our standardized fixed-effect coefficient estimates.

Model Testing and Projection- The LASSO and VIF tests indicated no issues with collinearity within my selected top model (Neter et al. 1996, Tibshirani 1996). The top model had a mean internal cross-validation estimate of 0.88 ± 0.004 (SE). The top model had an external cross-validation estimate of 0.97 ± 0.01 (SE).

Subpopulation characteristics.−Availability of forage and exposure to predation varied widely across subpopulations (Table 3). Strength of selection for forage varied across subpopulations, however, I found no evidence of a relationship between availability and strength of selection for herbaceous vegetation (r =0 .02, P= 0.79) and very low evidence for barren vegetation (r =0.19, P= 0.20). I found no evidence of a relationship for avoidance of predation encounter risk (r =0.06, P= 0.61). I did, however, find a strong and positive relationship between availability and selection of proximity to escape terrain (r =0.55, P= 0.06). Subpopulations with an abundance of habitat near to escape terrain within their spring home range had greater strength of selection for escape terrain (Figure 3).

DISCUSSION

I evaluated how lactating females balance forage acquisition and safety from predators during the early neonatal lambing period. I found support for the hypothesis that lactating females selected for habitat that minimized risk of predation on vulnerable neonates. As predicted, females strongly avoided habitat with increased risk of predation despite reduced access to high quality forage. Females showed strong avoidance of habitat with increased probability of encountering a hunting lion and selected strongly for habitat near escape terrain where visibility was high (open vegetation types). I further sought to test for a functional response across subpopulations between strength of selection and availability of forage resources and exposure to risk of predation. I found low variation in selection strengths across forage resources and predation encounter risk, despite wide variation in availability, indicating no evidence of a functional response. However, counter to my predictions, I found strong evidence of a positive functional response for low distances to escape terrain, indicating that subpopulations with greater proportions of safe terrain demonstrate stronger selection for it.

The strong correlation between predation risk and forage prevented me from directly testing for an interaction between forage biomass and risk. I hypothesize that the strength of the relationship is likely ultimately driven by the spatial distribution of mule deer. The seasonal distribution of mule deer populations is strongly linked to spatial forage biomass (Wickstrom et al. 1984, Marshal et al. 2004, Montieth et al. 2011), and because mule deer are the primary prey for mountain lions in the Sierra Nevada, lions distributions are strongly driven by the distribution of mule deer (Johnson et al. 2013). I also found that predation risk was higher in herbaceous vegetation types than barren types, indicating that where forage is presumed most abundant risk of encountering a hunting mountain lion is also greater.

Overall, the behavior of lactating bighorn sheep suggests risk of predation was strongly reduced by avoiding areas where the probability of encountering predators was high, distances far from escape terrain and areas where visibility was decreased. Females showed avoidance of areas with increased probability of encountering predators, such as low elevations, mild slopes and near waterways. Females also reduced predation risk by selecting habitat near escape terrain where they can quickly access terrain that is predator are less likely to be able to navigate. By selecting habitat with increased visibility, lactating females can detect approaching predators and decrease the risk of mortality.

Consequently, to remain safe from predation females must compromise access to high quality nutrition during the early neonatal period. The strong positive correlation I observed between predation risk and forage biomass suggests that access to forage biomass is decreased when sheep select habitat where predation risk is relatively low. Predation risk and forage quality was lowest at high elevations where green-up is delayed and mountain lions are infrequent. Previous work by Wehausen et al. (1995), Greene et al. (2010), and comparable research on alpine vegetation by Rachlow and Bowyer (1998) and Hamel and Côté (2007) indicates that measures of digestibility and crude protein are lowest in areas immediately surrounding escape terrain. I hypothesize that to maintain forage intake, females may choose to forage on alternative plant species that are more readily available at higher elevations near escape terrain, thus explaining the unexpected positive selection for shrubs. Selection for shrubs was not universal across the landscape however and depended strongly on predation risk; when risk was low, selection for shrubs increased. Females may choose to forage on shrubs because they are abundantly available within habitat where predation risk is relatively low and fresh annual growth can provide some nutritional value (Greene et al. 2012). Selection for barren vegetation types strongly increased with increasing predation risk, suggesting that females may be selecting for open habitat to forage in as predation risk increases. I hypothesize that risk of mortality from predators does not increase in barren vegetation types greatly due to the ability of sheep to detect predators, despite increased risk of encounters.

I found support for the hypothesis that variation in selection for forage resources and avoidance of predation risk between subpopulations could be explained primarily by differences in resource availability, indicating no functional response to these resources. However, I did find strong evidence to suggest that individuals within subpopulations responded to increased availability of low distances to escape terrain with increased selection for that terrain. This was in contrast to my prediction of a negative functional response, where a reduction in availability of safe terrain would result in increased selection for it. In a post-hoc examination I hypothesized that because overall risk of mortality from predation a function of encountering a predator and probability of evasion, selection strength for low distance to escape terrain (habitat that enables the evasion of predators) may depend on the availability of low distance to escape terrain as well as the overall risk of encountering a predator. I found a strong positive relationship between proportion of high encounter risk terrain and selection for proximity to escape terrain ($r= 0.55$, $p= 0.05$), indicating that for subpopulations with greater proportions of high encounter risk terrain, selection for ‘safe’ terrain was also greater. For example, Mt. Gibbs had the lowest selection coefficient (1.08), lowest proportion of low distance to escape terrain (35.1%), and lowest proportion of terrain with high predation (encounter) risk (7.2%). Wheeler Ridge had a selection coefficient 3 times higher (3.08), had 38% more availability of low distance to escape terrain (57.1%), and had 74% more terrain with of high risk of predation compared to Mt. Gibbs. Conner et al. (2018) concluded that Mt. Gibbs had one of the lowest occupancy rates of mountain lions, whereas Wheeler Ridge had one of the highest. I hypothesize that these differences in overall risk of predation may influence the ability of lactating females to obtain high quality nutrition. Montieth et al. (2018) found that females in Mt. Gibbs had the highest fall IFBFat (approximately 13.5%) of any subpopulation, whereas Wheeler Ridge, had among the lowest IFBFat of any subpopulation (approximately 10.5%).

Availability and selection of habitat during the early neonatal period can strongly influence the reproductive success of maternal ungulates and survival of neonates. Investigations into the adaptive strategies of ungulates to balance forage acquisition and predation risk have yielded diverse results that often provide conflicting management implications. Evaluating how lactating females cope with the increased nutritional demands of lactation and increased vulnerability of neonates to predators is important for developing strategies for recovering small or endangered populations. Furthermore, identifying factors that influence selection of habitat can improve our understanding of the risk factors lactating females and neonates face and enable the development of effective management strategies.

I demonstrated that predation risk was a strong driver influencing the selection of neonatal lambing habitat, however my estimates of predation risk were based on an ambush predator, which are considered more spatially predictable than coursing predators because of their requirement for visual cover to hunt (Heithaus et al. 2009, Middleton et al. 2013, Blake and Gese 2016). I hypothesize, however, that my definition of escape terrain also served as habitat that is safe from coyotes because coyotes are also unlikely to be successful at hunting sheep in such steep slopes. I was unable to estimate spatial risk from avian predators such as golden eagles.

Understanding the availability of high quality lamb rearing habitat is an important consideration in restoring bighorn populations. My results demonstrate that resource availability and abundance of high quality lambing habitat differs across subpopulations. Differences in abundance and connectivity of lambing habitat may be important in understanding differences in lamb recruitment and population performance among subpopulations. Furthermore, quantifying the proximity of lamb rearing habitat to summer and winter ranges aids in predicting the success of current and future subpopulations. My models will assist managers in identifying habitat that is most likely to meet the lambing needs of lactating bighorn sheep and facilitate recovery.

MANAGEMENT IMPLICATIONS

By incorporating my findings into future reintroduction plans, managers of Sierra Nevada bighorn sheep can evaluate the suitability of neonatal lamb rearing habitat within potential reintroduction sites (Appendix C). Recolonization into historic ranges and connectivity between Sierra bighorn sheep subpopulations is a key component in species recovery and ensuring long-term viability of fragmented subpopulations. My predictive maps could inform spatial prioritization for the establishment of Sierra bighorn sheep habitat relative to neonatal lamb rearing habitat within the Sierra Nevada range (Figure 4). In established subpopulations, managers could evaluate augmentations based on predation risk relative to increased visibility and increased forage opportunities.

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Table 1. Predictor variables hypothesized to affect selection of habitat by lactating Sierra Nevada bighorn sheep in the Sierra Nevada of California, USA during the neonatal lambing period from 2006–2017.

Habitat Variable	Biological Association	Variable Description
NDVI	Temporal plant phenology index (Pettorelli et al. 2007, Hamel et al. 2009, Sensi et al. 2012)	Continuous (reflective units) derived from MODIS
Relative probability of encountering a mountain lion	Mountain lion predation risk (Appendix A)	Continuous (relative probability 0–99%)
Vegetation cover: Tree	Low visibility with high risk of encountering ambush predators, no nutritional value	Indicator, derived from thematic vegetation layers from CalVEG
Vegetation cover: Shrub	Medium visibility, moderate risk of encountering ambush predators, annual woody vegetation with low digestibility and crude protein	Indicator derived from thematic vegetation layers from CalVEG
Vegetation cover: Herbaceous	High visibility perennial meadows with the largest biomass of forbs, graminoids and cushion plants available in the study area	Indicator derived from thematic vegetation layers from CalVEG
Vegetation cover: Barren	High visibility, open rocky terrain with intermittently dispersed sparse graminoids and forbs	Indicator, derived from thematic vegetation layers from CalVEG
Closed Terrain	Low visibility, high risk of encountering ambush predators (Hornocker 1970, Holem and Laundre 2006, Kunkel et al. 2013, Blake and Gese 2016)	Indicator (barren and herbaceous cover types)
Distance to trail/road	Human influence (Smith et al 2015)	Continuous (0–max: 1,200meters)
Distance to water	Potential sources of hydration	Continuous (0–max: 1,200meters)
Elevation	Vegetation communities and temperatures regimes	Continuous (0–4,660 meters)
Elevation+ Elevation^2	Quadratic to represent selection of intermediate values	
Slope	Predator success, used to define Escape Terrain	Continuous (0–90 degrees)
Slope+ Slope^2	Quadratic to represent selection of intermediate values	

Distance to escape terrain	Distance to habitat safe from predators (Appendix A; Fairbanks et al. 1987, Harris et al. 1995).	Escape terrain: slopes ≥ 42° Binned (Low: 0–120m, Med: 121–240m, High > 241)
Topographic Position Index (TPI)	Measure of ruggedness	Continuous index (-180: 180)
TPI+ TPI^2	Quadratic to represent selection of intermediate values	
Solar Radiation Index (SRI)	Measure of solar radiation indicating exposure during spring (Pierce et al. 2005).	Continuous (kilowatt/hour) derived for latitude:37.5
Aspect	Measure of temperature and moisture. SE slopes are warmest during spring (Cuishman and Wallin 2002)	Continuous (0:NW–1:SE)

Table 2. Top mixed-effect models of resource selection function models evaluating selection of habitat by lactating Sierra bighorn sheep during the early neonatal period the Sierra Nevada of California, USA from 2006–2017. I considered models within 2 ΔBIC to be competitive; *k*= number of estimable parameters, LL=log-likelihood, ΔBIC=difference between the model listed and the BIC of the best model, ω_i= Akaike weights; BASE includes Low distances to escape terrain (0–120m), medium distance to escape terrain (120–240m), Predation Risk (relative probability of encountering a hunting mountain lion), Barren=(vegetation type with high visibility and sparse forage), Herbaceous (vegetation type with good visibility and high forage availability), Shrub (vegetation type with medium visibility and minimal forage); TPI= topographic position index, a measure of ruggedness; SRI=solar radiation index (kilowatt per hour); Aspect= continuous from 0 (NE) to 1 (SW).

Model	K^a	LL^b	ΔBIC^c	ω_i^d
BASE+ TPI+ Aspect	10	-79426	0	0
BASE+TPI	9	-79530	131	0
BASE+TPI+ SRI	10	-79548	278	0
BASE+Aspect	9	-79798	302	0
BASE	8	-79882	803	0

Table 3. Estimated percent composition of available habitat variables within spring ranges for seven Sierra Nevada bighorn sheep subpopulations in the Sierra Nevada of California from 2006–2017. Percentages were calculated from randomly available locations systematically sampled within each spring home range (Benson 2013).

Habitat Resource		Warren	Gibbs	Convict	Wheeler	Sawmill	Baxter	Langley
Vegetation type	Tree	23.7	19.9	10.7	18.7	20.9	11.2	26.7
	Shrub	11.2	7.7	13.6	36.3	25.0	11.0	19.8
	Herb	7.5	9.0	2.8	1.4	1.5	27.5	5.8
	Barren	57.7	63.4	72.9	43.6	52.6	50.2	47.6
Distance to escape terrain	Low	35.6	35.1	54.2	57.1	48.2	49.4	45.7
	Med	25.5	20.6	26.0	17.8	22.4	22.4	21.3
	High	39.0	44.3	19.9	25.0	29.4	28.2	33.1
Relative lion predation risk	Low	73.8	86.2	74.8	54.8	59.4	59.6	59.5
	Med	12.4	6.6	10.0	17.8	10.8	15.8	11.6
	High	13.8	7.2	15.2	27.4	29.8	24.6	28.8
99% KDE Subpopulation Spring Home range (km^2)		6.63	3.32	2.15	10.03	9.12	8.68	8.74

Table 4. Standardized coefficients and standard errors from the top generalized linear mixed-effect model fit to determine selection of habitat by lactating Sierra bighorn sheep during the early neonatal period in the Sierra Nevada of California, USA from 2006–2017. The individual-level variation (n=123, SD <0.001) and subpopulation-level variation (n=7, SD= 0.01). Low Distance Escape Terrain= habitat <120m from escape terrain (slopes> 42°); Med Distance Escape Terrain= habitat between ≥120m and <240m from escape terrain; LionRisk = relative probability of encountering a hunting mountain lion; Barren=sparse grasses and forbs ; Shrub=shrub vegetation ; Herb=herbaceous vegetation ; Topographic Position Index= index of directional ruggedness

Model Covariate	ß-coefficients
Intercept [a]	-3.89 (0.05)
Low Distance Escape Terrain	2.30 (0.03)
Med Distance Escape Terrain	1.15 (0.03)
Lion Encounter Risk	-0.64 (0.01)
Barren	0.85 (0.02)
Shrub	0.82 (0.03)
Herb	0.31 (0.04)
Topographic Position Index (TPI)	0.09 (0.003)
LionRisk*Barren	0.70 (0.02)

[a] Intercept contains the reference categories: high distance to escape terrain and tree vegetation

Figure 1. Study area for Sierra Nevada bighorn sheep in southeastern Sierra Nevada range of California, USA from 2006–2018. Herds extend from Mt. Warren near Lee Vining, CA south approximately 200 km to Olancha, CA. Study subpopulations are outlined in orange and include: Mt. Warren, Mt. Gibbs (Northern Recovery Unit); Convict Creek, Wheeler Ridge (Central Recovery Unit); Mt. Baxter, Sawmill Canyon and Mt. Langley (Southern Recovery Unit).

Figure 2. Resource selection by lactating Sierra Nevada bighorn sheep during the early neontal period in the Sierra Nevada of California, USA from 2008–2017 displaying the relative probability of selection for encountering a mountain lion by vegetation category.

Figure 3. Functional response of seven subpopulations of lactating Sierra Nevada bighorn sheep during the early neontal period in the Sierra Nevada of California from 2008-2017 displaying the relative probability of selection for low distances to escape terrain (0-120 m) against the proportional availability of low distances to ecape terrain Selection moderately increased for all subpopulations with increasing availability of low distances to escae terrain.

Figure 4. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep developed from 123 animal-years across seven subpopulations in the Sierra Nevada of California between 2008 and 2017 from a used-available resource selection function. Predicted selection is displayed across all occupied and currently vacant subpopulations. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure 1.

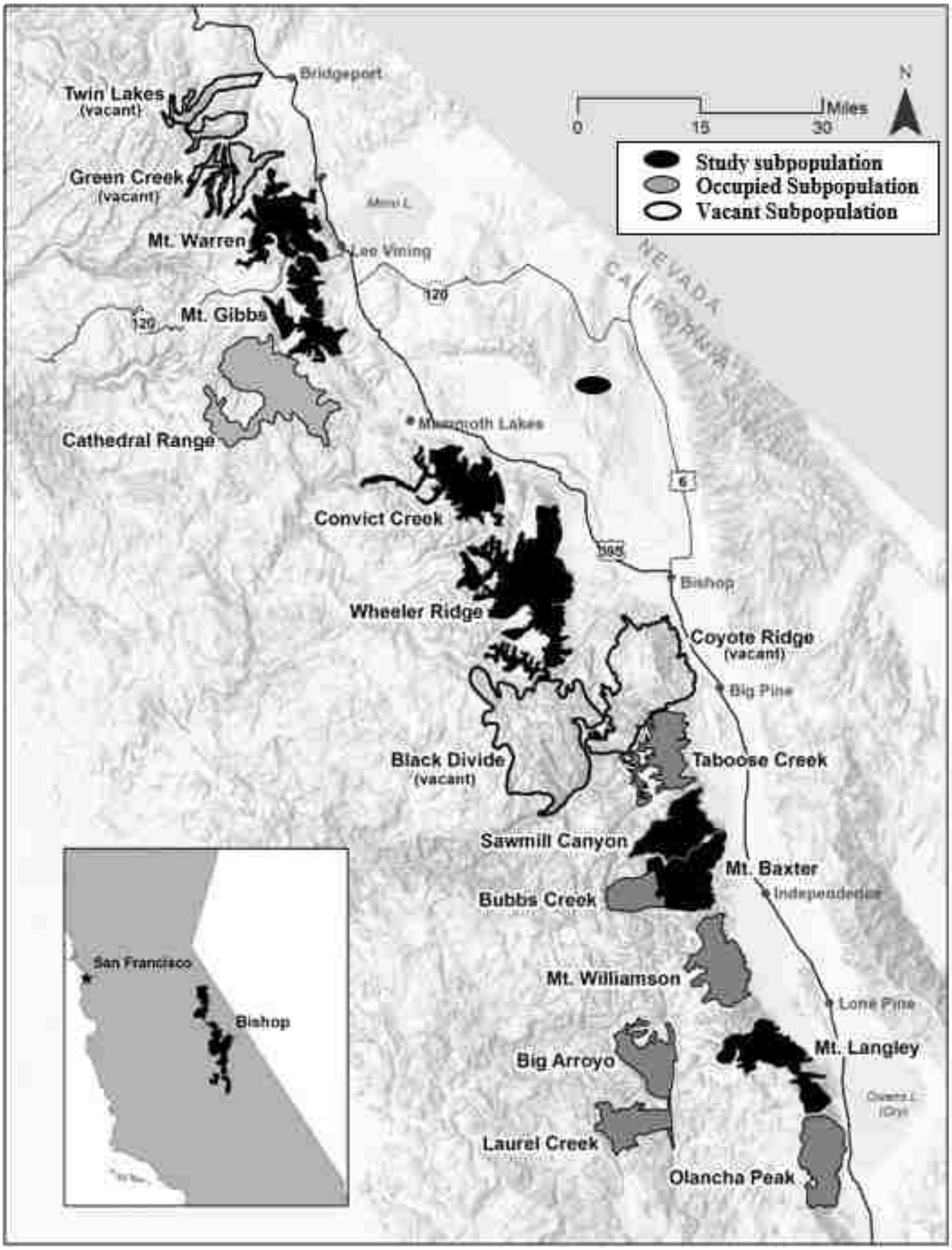

Twin Lakes
(vacant)
Bridgeport
0
15
30
Miles
N
Study subpopulation
Occupied Subpopulation
Vacant Subpopulation
Green Creek
(vacant)
Mono L.
Mt. Warren
Lee Vining
NEVADA
CALIFORNIA
120
120
Mt. Gibbs
Mammoth Lakes
Cathedral Range
6
Convict Creek
395
Bishop
Wheeler Ridge
Coyote Ridge
(vacant)
Big Pine
Black Divide
(vacant)
Taboose Creek
Sawmill Canyon
Mt. Baxter
Independence
Bubbs Creek
Mt. Williamson
Lone Pine
Mt. Langley
Big Arroyo
Owens L.
(Dry)
Laurel Creek
Olancha Peak
San Francisco
Bishop

Figure 2.

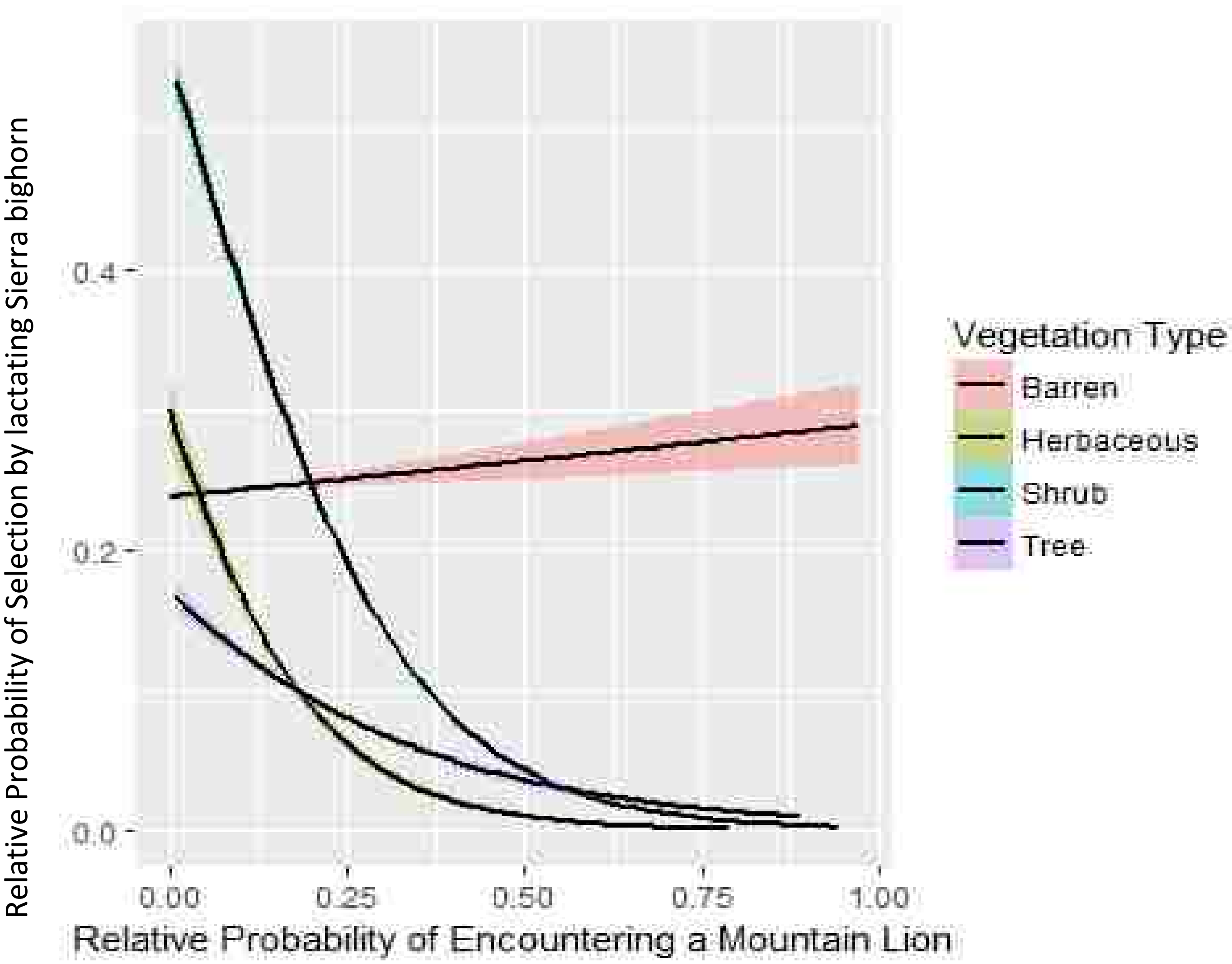
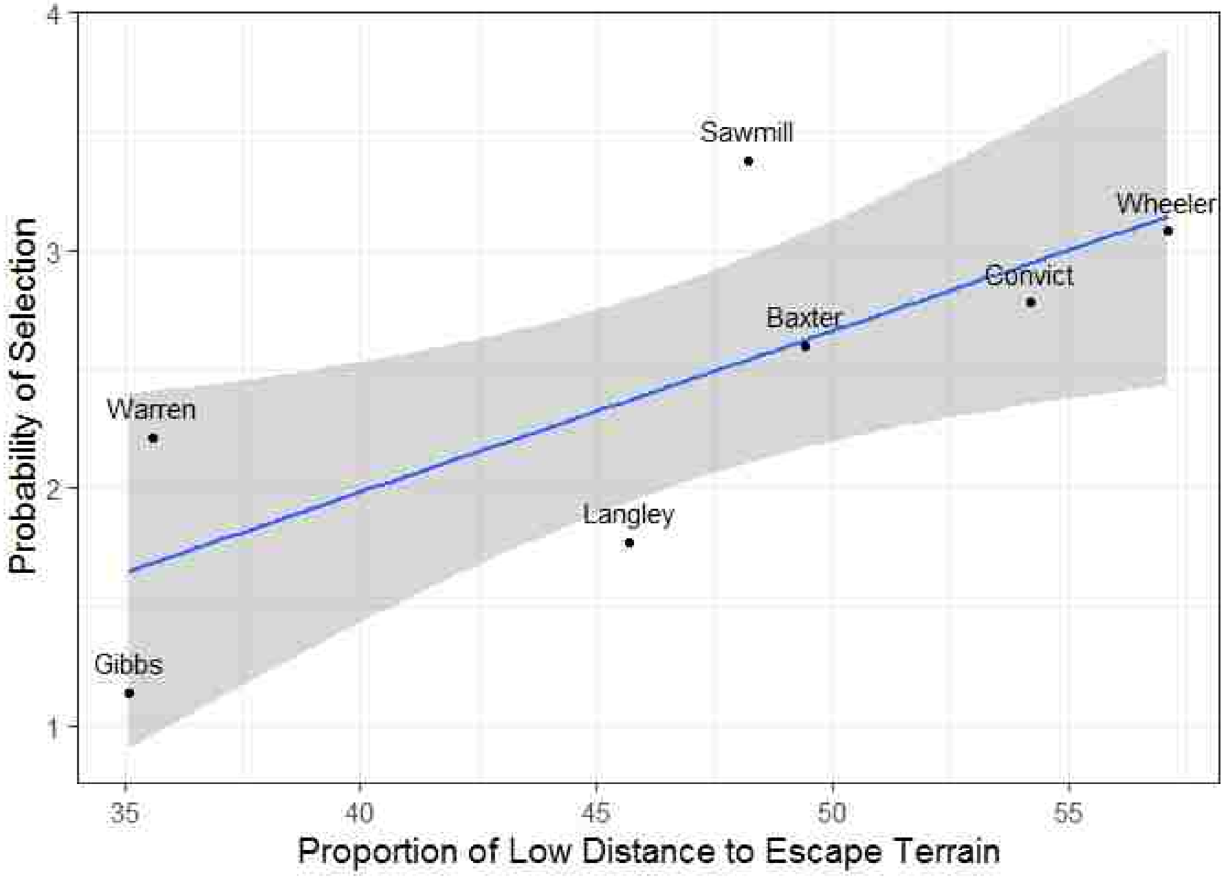
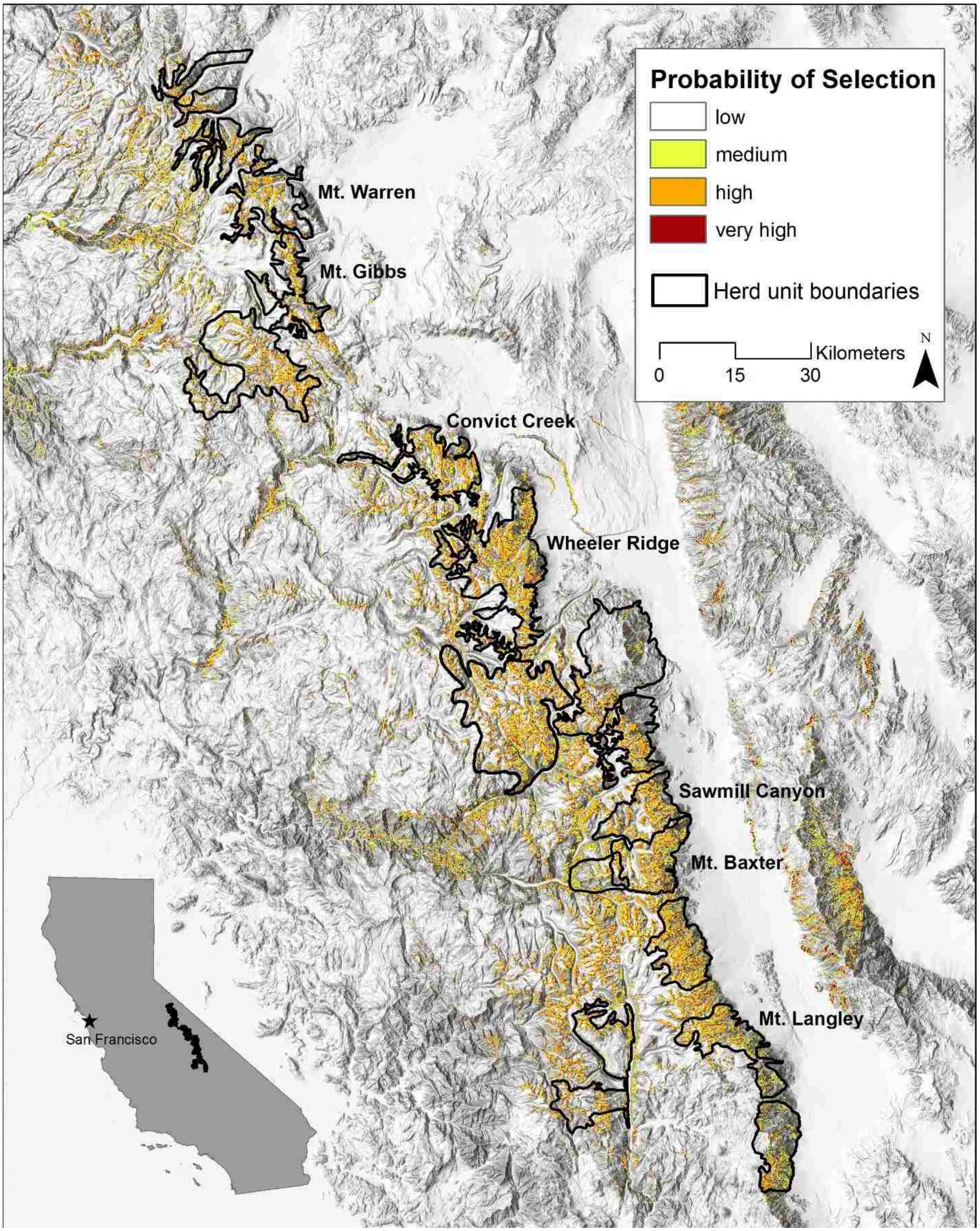

Relative Probability of Selection by lactating Sierra bighorn
0.0
0.2
0.4
0.00
0.25
0.50
0.75
1.00
Relative Probability of Encountering a Mountain Lion
Vegetation Type
Barren
Herbaceous
Shrub
Tree

Figure 3.



Sawmill
Wheeler
Convict
Baxter
Warren
Langley
Gibbs
4
3
2
1
35
40
45
50
55
Probability of Selection
Proportion of Low Distance to Escape Terrain

Figure 4.


Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
15
30
Kilometers
N
Mt. Warren
Mt. Gibbs
Convict Creek
Wheeler Ridge
Sawmill Canyon
Mt. Baxter
Mt. Langley
San Francisco

APPENDIX A: PARTURITION DETECTION ALGORITHM

I developed a cluster detection algorithm using the adehabitatHR package (Calenge 2006) in Program R (R Core Team 2018) to determine parturition dates of female Sierra Bighorn sheep from 2008-2018. I developed input criteria for the algorithm using GPS locations and vaginal implant transmitters (VITs; (DeMars et al. 2013, McGraw et al. 2014, McClintock et al. 2012, 2014, Blackwell et al. 2016). I included a sub-sample of adult females (n=22) fitted with high fix-rate GPS collars and VITs during spring captures. Once a VIT was expelled, I visually verified the birth event and monitored the movement patterns of females and offspring. I then calculated the average time spent in a parturition site, and the average distance traveled from the location the VIT was expelled.

I found females spent on average ($\bar{\chi}$ = 26, SE= 4) hours in a parturition site and remained within an average of ($\bar{\chi}$ 19m, SE= 11m) from the site until departing. I used these parameters to predict independent visually-verified parturition sites for females with variable fix-rate GPS collars that did not receive VITS (n=21). I tested for false positives (clustered GPS locations that are not the result of parturition) using GPS data from females that were not pregnant. I found these methods of parturition detection correctly identified all independently verified parturition sites and did not result in any false positives (no potential clusters were identified) for females that were not pregnant.

I determined potential parturition dates for the remaining sample of females (n= 80) using the range of times and distances estimated from the VIT females (Figure 1). I used three criteria to externally evaluate whether clusters identified by the algorithm could be considered parturition sites. First, each cluster must have included locations during daylight hours when a sheep would normally be expected to exhibit foraging behavior (approximately 07:00am to

6:00pm). Second, each cluster must have been preceded by movement greater than the average daily movement for that female, a long-distance movement from winter range, or movement away from other collared females. Finally, I cross-referenced visual observations of females to be sure that no offspring were observed with a female prior to the predicted cluster date. In some cases, I was also able to confirm a lamb had been observed after the predicted parturition date; however, due to potential offspring mortality, this was not a required criteria. I found no discrepancies between visual observations and predicted parturition dates. In addition to these criteria, I also mapped predicted cluster locations and checked local weather conditions to reduce uncertainty. If there were sequential clusters that fit the aforementioned criteria, the earliest date was selected because Sierra bighorn are known to remain localized in a parturition site then make a small movement to a nursery site (Figure A1).

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R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/.

R code: Cluster Detection Algorithm

Install packages and set working directory and other preferenes.

```
install.packages("fpc", dependencies = TRUE, repos = "http://cran.us.r-proje
ct.org")

library(adehabitatHR)           # Load package

library(RODBC)
library(gtools)

library(fpc)

setwd("C:/Users/SForshee/Desktop/Lambing_Clusters") # Redefine directory
#rm(list=(ls()))                        # clears memory by deleting all variab
les
#graphics.off()                     #close graphics window
```

Connect to database and retrieve GPS location data. The following code is specific to each database where the GPS data resides, and is set-up for Sierra bighorn sheep.

```
bhdb<-file.path("bighorn.mdb")            # Identify database
channel<-odbcConnectAccess(bhdb)            # Open connection

##  AllCollarLocations  ##                  # Pull table from access and modif
y
##======================##
acl.raw=sqlFetch(channel,"AllCollarLocations",colnames=F,rownames=F)
nrow(acl.raw)

## [1] 1346929

odbcClose(channel)                    # Close connection

acl=acl.raw[-grep("d",acl.raw$AnimalID,ignore.case=T),] # Remove Desert Sheep
acl$AnimalID=factor(gsub("S","s",acl$AnimalID))             # Standardizes cap
italization for AnimalID
nrow(acl)

## [1] 1337663

unique(acl$AnimalID)

##   [1] s191 s210 s211 s213 s225 s226 s231 s236 s241 s243 s246 s251……
```

Enter the animal ID ("ID") exactly as it appears in the database, the year "YYYY", the month range starting "MM" & ending "MM".

```
ID="s465"                                       ### Enter animal ID ###
cl<-acl[which(acl$AnimalID==ID),]
head(cl)
```

```
##         AnimalID     Date    UTM_E   UTM_N Method     Time DOP SV Fix
## 1214549     s465 20170322 384495.9 4085622      V 00:00:39 9.2     3D
## 1214565     s465 20170322 384506.8 4085616      V 04:00:40 5.2     3D
## 1214581     s465 20170322 384471.8 4085627      V 08:00:39 2.2     3D
## 1214600     s465 20170322 384466.5 4085618      V 12:00:39 3.6     3D
## 1214620     s465 20170322 384472.6 4085629      V 16:00:39 2.0     3D
## 1214630     s465 20170322 384472.1 4085626      V 20:00:39 3.0     3D
##                     keyfield CollarSerialNo_Date_FK HU RU Sex
## 1214549 2017032200:00:39S465         23266_20170320 Bx  S   F
## 1214565 2017032204:00:40S465         23266_20170320 Bx  S   F
## 1214581 2017032208:00:39S465         23266_20170320 Bx  S   F
## 1214600 2017032212:00:39S465         23266_20170320 Bx  S   F
## 1214620 2017032216:00:39S465         23266_20170320 Bx  S   F
## 1214630 2017032220:00:39S465         23266_20170320 Bx  S   F
```

```
nrow(cl)
```

```
## [1] 2930
```

```
cl$year<-substring(cl$Date,1,4)
cl<-cl[which(cl$year=="2017"),]                 ### Enter year ###
cl$month<-substring(cl$Date, 5,6)
cl<-cl[which(cl$month>="04" & cl$month<="08"),] ### Enter month range ###
cl<-cl[order(cl$Date & as.numeric(cl$Time)),]
cl$row<-1:nrow(cl)
head(cl)  # review for completeness
```

```
##         AnimalID     Date    UTM_E   UTM_N Method     Time DOP SV Fix
## 1215738     s465 20170401 384868.0 4085589      V 00:00:39 2.2     3D
## 1215746     s465 20170401 384864.3 4085589      V 02:00:08 2.8     3D
## 1215764     s465 20170401 384865.3 4085591      V 04:00:39 2.4     3D
## 1215775     s465 20170401 384860.7 4085525      V 06:00:38 5.8     3D
## 1215798     s465 20170401 385000.0 4085522      V 08:00:40 1.8     3D
## 1215808     s465 20170401 385032.9 4085506      V 10:00:08 4.8     3D
##                     keyfield CollarSerialNo_Date_FK HU RU Sex year month
## 1215738 2017040100:00:39S465         23266_20170320 Bx  S   F 2017    04
## 1215746 2017040102:00:08S465         23266_20170320 Bx  S   F 2017    04
## 1215764 2017040104:00:39S465         23266_20170320 Bx  S   F 2017    04
## 1215775 2017040106:00:38S465         23266_20170320 Bx  S   F 2017    04
## 1215798 2017040108:00:40S465         23266_20170320 Bx  S   F 2017    04
## 1215808 2017040110:00:08S465         23266_20170320 Bx  S   F 2017    04
##         row
## 1215738   1
## 1215746   2
## 1215764   3
## 1215775   4
## 1215798   5
## 1215808   6
```

The follow step allows you to calcualte the averages fixes per day based on the time frame set above. This will be important when setting the minimum number of fixes to be considered a cluster. I recommend using the output from this command as the input for the first cluster paramter (“fixrate”) rather than the expected number of fixes based on collar settings.

```
(fixes.est<-nrow(cl)/length(unique(cl$Date))) ### Calculates fixes per day
```

```
## [1] 9.059211
```

This section organizes the location data, and does not need to be modified.

```
data<-cbind(cl$UTM_E,cl$UTM_N,cl$Date,as.character(cl$Time))
colnames(data)<-c("UTM_E","UTM_N","Date","Time")
data<-as.data.frame(data)
data$UTM_E<-as.numeric(as.character(data$UTM_E))
data$UTM_N<-as.numeric(as.character(data$UTM_N))
data$Date<-as.numeric(as.character(data$Date))
data<-as.data.frame(data)
```

Set the cluster search parameters. These should be set based on 2 criteria:

A) Basic biology of the species. For Sierra bighorn sheep, I expect a female to remain in a parturition site on average for a MINIMUM of 18 hours, staying within MAXIMUM radius of 40 meters. A female may remain much longer than 18 hours, and may remain within a much tighter radius, but these parameters provide a basic starting point for the minimum requirements to be considered a parturition site.

B) Biological parameters must be then tailored to fit the GPS fix rates and local conditions. The

- "fixrate" is the number of locations per 24 hour period
- "ndays" is the consecutive number of days to search for a cluster, a day begins at 00:00 and ends on 23:59, thus if a sheep enters a parturition site at hour 20:00, a second day will be needed to be considered a cluster (two to three days is optimal for this parameter)
- "fixperperiod" is the "fixrate*ndays" and results in the total number of points possible to be within a cluster
- "eps" is the Euclidian diameter size in meters of a the search area,
- "minpts" is the minimum number of GPS locations that must be contained within the eps distance.

A final consideration is the completeness and accuracy of GPS data, although a collar may be programmed to take a fix 12 times per day, some fixes may be incomplete, this is why reviewing your dataset and calculating your average fixes per day is an important previous step. If the average fixes is lower than expected, I suggest reducing the number of minpts to account for potential missed fixes. Furthermore several factors can affect the precision of GPS fixes, rugged terrain and closed canopies can increase GPS fix errors, thus the eps setting may need to be adjusted based on local terrain, I also suggest estimating GPS accuracy for the specific collar company as these can vary.

For example the code below represents a female (s465) with a collar that records an estimated 12 fixes per day (a fix every 2 hours), 2 consecutive days of parturition would yield 24 possible fixes if none are missed. To search for a parturition cluster, a setting of eps=18, minpt=12 will provide result in a GPS cluster of 24 hours within 18m. However, because the average number of fixes previously calculated was 9, consider reducing the fix rate and subsequent "fixperperiod" calculation.

```
fixrate<-12          ### Number of fixes expected in a 24 hour period (day) ###
nday<-2              ### Search Period (Number of consecutive days) ###
```

```
fixperperiod<-24    ### Number of fixes possible in period (fixrate*ndays) ###


eps<-18             ### Maximum disatance of circle in meters  ###
minpt<-12           ### Minimum number of points within "eps"  ###
```

Run the cluster analysis, looping through the entire GPS dataset (“cl”) to identify groups of locations that fit the previously defined paramter criteria.

```
cnt<-1;cnt1<-1
cluster.all<-NULL; cluster.new<-NULL
iloop<-1

# loop through days  #
for (iloop in 1:200){   #test for overun of end of data    if((iloop*fixrate+f
ixperperiod)>nrow(cl)) {
    upper<-nrow(cl)
  }else{
    upper<-iloop*fixrate+fixperperiod
  }
  data.sub<-as.data.frame(data[((iloop*fixrate-fixrate+1):upper),c(1:3)])  #1:
3 is x,y corrd, and date units. 1:2 is just x,y
    data.sub<-na.omit(data.sub)
  cl.sub<-cl[((iloop*fixrate-fixrate+1):upper),]
  names(data.sub)<-c("UTME","UTMN","Date")
  d <- dbscan(data.sub,eps=eps,MinPts=minpt,showplot = 0)          # Calls D
BSCAN routine ;eps = Euclidan distance and MinPts (default=5).#can show graphi
c of UTMs using showplot=T
  if(sum(d$cluster)>0) {
    cluster.new<-as.data.frame(cbind(rep(cnt,length(d$cluster)),d$cluster,cl.s
ub$Date,cl.sub$UTM_E,cl.sub$UTM_N,as.character(cl.sub$Time)))
    cluster.new<-cluster.new[which(cluster.new[,2]!=0),]
    cluster.new<-cluster.new[,-2]
    cluster.all<-rbind(cluster.all,cluster.new)
    cnt<-cnt+1
    cluster.new<-NULL}
}
```

View the print out of clusters. “Iteration” refers to a cluster number, “Date” refers to the date of the GPS location, “UTME” refers to the Easting of the location, “UTMN” refers to the Northing of the location," Time" refers to the time stamp from the local time zone in 24 hour format, where 00:00 refers to midnight and 12:00 will be noon.

```
names(cluster.all)<-c("iteration","date","UTME","UTMN","Time")
options(max.print=2000) ####some clusters or sequences can be large, if you r
each max of 2000, constrict your parameters
print(cluster.all[order(cluster.all$date, cluster.all$iteration),])
```

Several clusters may contain the same GPS locations, this will depend on the previous formatting of sequential days specified for the cluster search. For example a single GPS location may be included in several Iterations if it meets the minimum requirements specified for a cluster with the inclusion of nearby locations that alone do not constitute a cluster. Each iteration (cluster) will receive a new number, but several clusters may overlap. This is NOT an error and can instead indicate several clusters that are near enough to share points, alternatively the same large cluster may meet the minimum requirements with only a portion of the locations that make up the total cluster. See highlighted example below:

```
##      iteration     date     UTME    UTMN     Time
## 7            1 20170413 382303.4 4082570 14:00:38
## 9            1 20170413 382297.3 4082547 20:00:40
## 10           1 20170413 382304.8 4082562 22:00:38
## 11           1 20170414 382306.8 4082555 00:00:38
## 12           1 20170414 382311.4 4082556 02:00:40
## 13           1 20170414 382307.2 4082564 04:00:40
## 14           1 20170414   382315 4082554 06:00:38
## 15           1 20170414 382324.2 4082573 07:14:27
## 16           1 20170414 382333.5 4082558 08:00:38
## 22           1 20170414 382320.4 4082559 20:00:39
## 1            2 20170414 382307.2 4082564 04:00:40
## 2            2 20170414   382315 4082554 06:00:38
## 3            2 20170414 382324.2 4082573 07:14:27
## 4            2 20170414 382333.5 4082558 08:00:38
## 5            2 20170414 382339.3 4082555 10:00:40
## 6            2 20170414   382337 4082568 12:00:38
## 71           2 20170414 382343.5 4082548 14:00:37
## 8            2 20170414 382345.9 4082556 16:00:09
## 91           2 20170414 382343.2 4082547 18:00:39
## 101          2 20170414 382320.4 4082559 20:00:39
```

The time stamp should be reviewed critically before a cluster can be designated as parturition. Species biology and other external factors should be carefully considered. For example a cluster that only includes times of 20:00, 00:00, 02:00, 04:00, 06:00 is most likely an overnight bedsite, Sierra bighorn sheep often revisit a bedsite on consecutive days. Thus a cluster with 10 GPS locations with the specified distance over 2 days may technically fit the cluster criteria, this is unlikely to be a true parturition site. Sierra bighorn sheep often remain in in a parturition site during daylight hours, and are unlikely to move outside the cluster to feed for an extended period of time, thus daytime hours are important criteria for considering a cluster a parturition site.

In some cases, for Sierra bighorn sheep there may be a cluster at a parturition site and a secondary cluster immediately after that is considered a nursery site and will share similar patterns as the parturition site.

The following output code shows partial output from a parturition site (highlighted in yellow), a nursery site (highlighted in green) and an overnight bedsites that was re-used by a female consecutive nights (highlighted in red). This female made a long-distance movement into the parturition site on 04/13 around 14:00 and remained within the site for nearly 4 days departing on 4/17 around 10:00 when she moved into a nursery site, where she spent an additional 7 days until departing the site on the night of 4/23. She remained near the area until departing altogether on 4/26. The additional clusters below these dates are examples of repeated use bedsites that are not associated with parturition.

```
##      iteration     date     UTME    UTMN     Time
## 7            1 20170413 382303.4 4082570 14:00:38
```

```
## 9           1 20170413 382297.3 4082547 20:00:40
## 10          1 20170413 382304.8 4082562 22:00:38
## 11          1 20170414 382306.8 4082555 00:00:38
## 12          1 20170414 382311.4 4082556 02:00:40
## 13          1 20170414 382307.2 4082564 04:00:40
## 14          1 20170414   382315 4082554 06:00:38
## 15          1 20170414 382324.2 4082573 07:14:27
## 16          1 20170414 382333.5 4082558 08:00:38
## 5           2 20170414 382339.3 4082555 10:00:40
## 6           2 20170414   382337 4082568 12:00:38
## 71          2 20170414 382343.5 4082548 14:00:37
## 8           2 20170414 382345.9 4082556 16:00:09
## 91          2 20170414 382343.2 4082547 18:00:39
## 101         2 20170414 382320.4 4082559 20:00:39
## 24          1 20170415 382320.8 4082553 00:00:39
## 25          1 20170415 382313.1 4082556 02:00:37
## 26          1 20170415 382313.3 4082555 04:02:45
## 27          1 20170415 382313.4 4082552 06:00:38
## 51          5 20170417 382272.9 4082396 10:00:39
## 83          5 20170417   382239 4082409 16:00:40
## 94          5 20170417   382248 4082412 18:00:39
## 104         5 20170417 382247.9 4082406 20:00:40
## 112         5 20170417 382249.8 4082407 22:00:38
## 243         4 20170418 382247.9 4082407 00:00:38
## 253         4 20170418 382242.6 4082404 02:00:40
## 263         4 20170418   382251 4082404 04:00:38
## 324         9 20170423 382249.8 4082410 18:00:39
## 335         9 20170423 382247.4 4082404 20:00:40
## 346         9 20170423 382250.7 4082406 22:00:40
## 356         9 20170424 382252.4 4082388 00:00:39
## 366         9 20170424 382252.6 4082405 02:00:40
## 99         13 20170515 383946.7 4081704 18:00:39
## 1010       13 20170515 383945.5 4081689 20:00:39
## 1112       13 20170515 383953.1 4081695 22:00:38
## 1210       13 20170516 383951.9 4081695 00:00:39
## 1310       13 20170516 383944.6 4081692 02:02:39
## 1411       13 20170516 383947.4 4081689 04:00:40
## 2210       13 20170516 383955.6 4081680 20:00:39
## 239        13 20170516 383946.4 4081685 22:00:38
## 120        14 20170516 383944.6 4081692 02:02:39
## 230        14 20170516 383947.4 4081689 04:00:40
## 1011       14 20170516 383955.6 4081680 20:00:39
## 1113       14 20170516 383946.4 4081685 22:00:38
## 249        13 20170517 383947.4 4081684 00:00:39
## 2510       13 20170517 383947.4 4081682 02:01:30
## 2610       13 20170517 383952.7 4081690 04:00:38
## 337        13 20170517 383945.7 4081693 20:00:39
## 348        13 20170517 383930.8 4081690 22:00:14
## 1211       14 20170517 383947.4 4081684 00:00:39
## 1311       14 20170517 383947.4 4081682 02:01:30
```

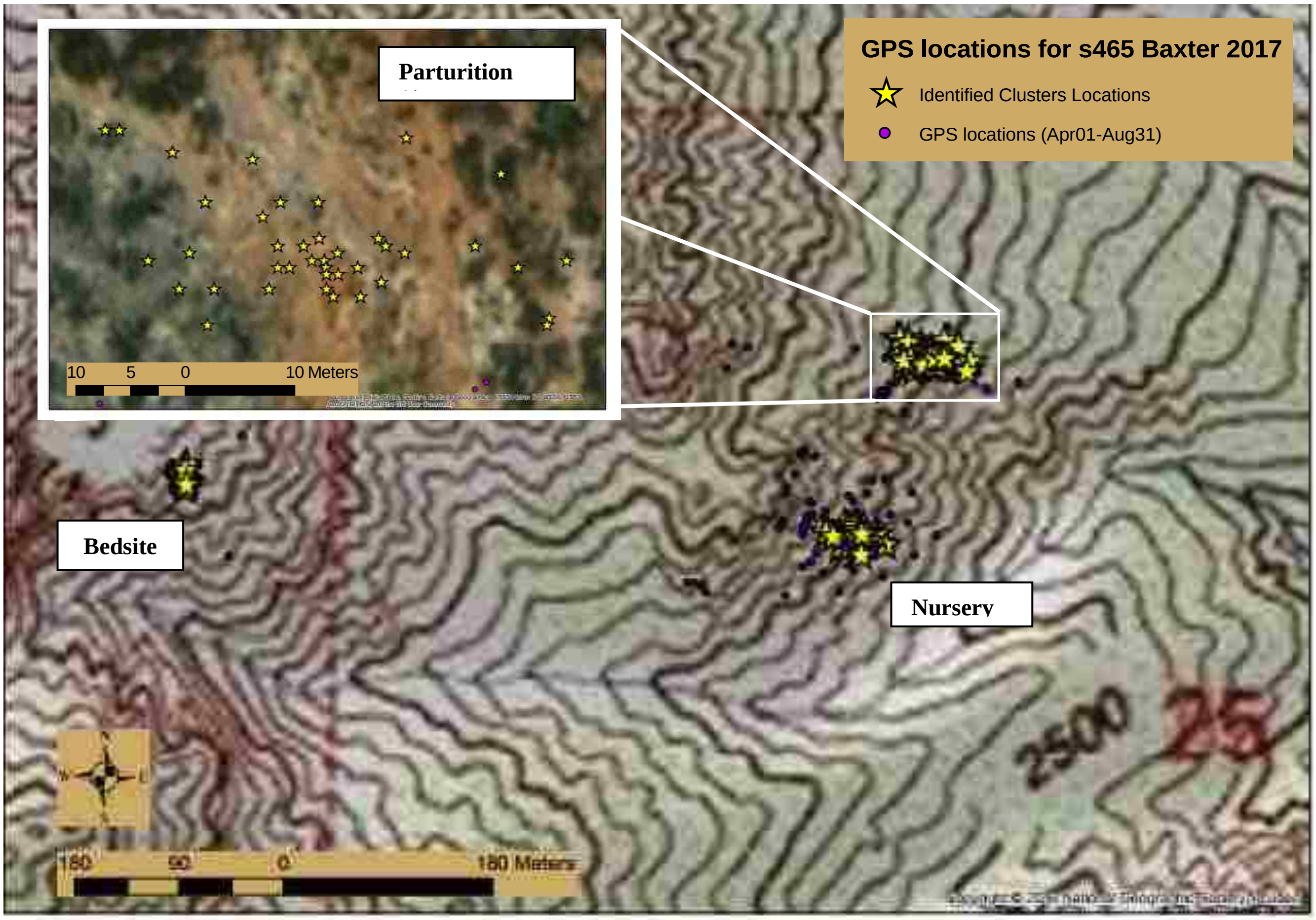
For Sierra bighorn sheep, it may also be important to check for spring storms that may cause sheep to cluster. This can be easily done using the following link: https://water.weather.gov/precip/

An additional way to estimate if a cluster is a parturition site is to map the locations by writing them to a csv or other file of your choice.

```
write.csv(cluster.all, "s465_2017parturition.csv")
```

Figure A1. Three GPS clusters identified by a cluster detection algorithm for an adult female Sierra Nevada bighorn sheep (s465) in 2017 in the Sierra Nevada of California. Based on post-identification parturition verification criteria, only one cluster (Inset map) is considered a parturition site where the females vaginal implant transmitter was expelled, the other large cluster is a post-parturition nursery site where the female and offspring moved to after several days in the parturition site, and the smallest cluster is a bedsite that was used for several consecutive nights.

Figure A1.



GPS locations for s465 Baxter 2017
☆ Identified Clusters Locations
● GPS locations (Apr01-Aug31)
Parturition
10 5 0 10 Meters
Bedsite
Nursery
2500
25
180 90 0 180 Meters

APPENDIX B. MOUNTAIN LION RESOURCE SELECTION FUNCTION

I developed a spatial model to predict the spatial probability of encountering hunting lions within Sierra bighorn sheep home ranges during spring at the third-order scale by developing a used-available resource selection function (RSF; Hosmer and Lemeshow 2000, Manly et al. 2002, Johnson et al. 2006). Predation risk is comprised of probability of encounter and probability of death (Hollings 1959), but perceived risk and subsequent behavior modifications by Sierra Nevada Bighorn sheep to avoid risk, may arise from simple encounters of mountain lions (Wehausen 1996). Mule deer (*Odocoileus hemionus*) are the primary prey of mountain lions in this region, but mountain lions are opportunistic hunters and are the cause of mortality for approximately 53% of all known Sierra bighorn sheep mortalities (California Dept. of Fish and Wildlife; CDFW, unpublished data). I quantified the relative probability of encounter risk by mountain lions across the Sierra Nevada and Owens Valley.

The portion of the Sierra Nevada that we studied extends along the Eastern border of California extending from Lee Vining, California in the north approximately 200 km south near Olancha, California (Hill 1975). Elevation changes abruptly along the Eastern front from 1000 m to an average of 3,000 m, with numerous peaks above 4,000 m. The strong rain shadow effect limits east of the Sierra crest and most of the annual precipitation falls as snow during winter months (November-April). The resulting xeric vegetation communities are separated by elevation classes, low-elevation (1500–2499 m) includes scrub with mixed grass and forb types; intermediate (2500–3300 m) includes moderate timber cover with sparse forbs and subalpine meadows; high elevations (>3300 m) includes sparse alpine vegetation (Hill 1975).

California Department of Fish and Wildlife crews captured mountain lions by pursuit with hounds and fitted them with GPS collars (see Pierce et al. 1998). I programmed collars to collect 6–10 GPS locations per day, with 5–7 locations during crepuscular and overnight hours (18:00–6:00) to best capture hunting behaviors.

I evaluated the relative probability of selection of habitat by mountain lions with a used-available resource selection function (RSF) within a logistic regression frame-work (Hosmer and Lemeshow 2000, Manly et al. 2002, Johnson et al. 2006). I used a 100% kernel density estimator (KDE) with 500m buffer (Worton 1989) to delineate available habitat for each mountain lion from April 1 –July 30th from all years. I sampled available locations within each individual mountain lion's home range, (Johnson 1980, Boyce 2006) using a 4:1 ratio of stratified random available locations to used GPS locations (Northrup et al. 2013).

I selected landscape attributes known from previous studies to influence mountain lion resource selection (Kunkel et al. 2013, Blake and Gese 2016, Justin Delinger, CDFW, unpublished data). I calculated topographic variables (slope, elevation, aspect, ruggedness) from 30m digital elevation models. I refined aspect using a geomorphology package in ArcGIS, such that 0 is warm dry aspect (southwest), and 1 is cooler shaded aspect (northeast). I condensed 6 landcover types (forest, shrub, alpine, desert, riparian, and water) obtained from thematic vegetation layers from CalVEG and calculated minimum distance to each for all pixels across the study area. I retained candidate variables that were non-confounded and screened for collinearity using the Pearson correlation coefficient threshold of $|r| \leq 0.6$ (Hosmer and Lemeshow 2000, Wickham 2009).

I considered additive, interactive, and quadratic term candidate models, and used a mixed-effects RSF allowing for heterogeneity across individual mountain lions (Gilles *et al.* 2006). I used a combination of graphical, Bayesian Information Criteria (BIC) guidelines, and ANOVA deviance values to determine the top model (Schwartz 1978, Boyce et al. 2002, Veneables and Ripley 2002, Hooten and Hobbs 2015). I evaluated the predictive performance of the top model using k-fold cross-validation (Boyce et. al 2002), using code provided by Brzustowski (2005). The predictive capacity of the partitioned model was evaluated against the withheld subset of data using Spearman rank correlations (r_s) grouped into 10 bins. I externally tested the top model using Spearman rank correlations from locations of mountain lion-killed sheep not included in model building compared to bins of predicted use. I mapped relative probability of use by mountain lions by multiplying the beta coefficients with each corresponding landscape attribute layer. I conducted all statistical calculations and graphical explorations in Program R 3.3.1 (R Core Team 2016) with packages: ‘adehabitatHR’, ‘maptools’, ‘rgdal’, ‘sp’, ‘raster’, ‘rgeos’, ‘spatial.tools’ , ‘MuMIn’, ‘MASS’, ‘GGally’, ‘ggplot2’ and ‘plotrix’, and ARC GIS 10.3.1 (ESRI 2011).

I collected 20,764 locations from 28 GPS-collared mountain lions that inhabited current and historical Sierra bighorn sheep distributions during the spring lamb rearing period (April-July) from 2002–2011. Mountain lions included eleven males and seventeen females, and eight were subadults. Each mountain lion’s collar collected between 2 and 12 fixes per day, most averaging 6 per day. Elevation, slope, ruggedness, aspect, and distance to vegetation cover types: desert, shrub, riparian, forest, and alpine barren, and distance to streams and seasonal drainages were consistently retained in top-ranked models (Table A1). Ruggedness was consistently ranked highly, but estimated beta coefficients and predictive mapping appeared incorrect. I determined that the method used to obtain ruggedness (Sappington *et al*. 2003), could provide misleading conclusions at the specified resolution. The resulting top model included the following fixed effect covariates and mountain lion ID (n=28) as a random effect (Table A2).

The mean Spearman rank correlation for the top model showed good model fit (rho=0.98) overall, and when partitioned by individual mountain lion (rho= 0.96). External validation from mountain lion-killed sheep (n=126) also showed good model fit (0.92). There were four mountain lions that the model did a poor job of predicting (rho <.50), two of which were subadult males. Individual differences in mountain lion selection accounted for less than 10% of model variation (0.07). Probability of mountain lion use was highest for elevations between 1,500–2,600 m. Probability of use was highest for slopes approximately 10–30° and dropped below 10% for slopes > 42°. Probability of use decreased for cooler and more shaded aspects (28%). Probability of use increased with increasing distance from alpine landcover types (27%), decreased with increasing distance from forest (68%), riparian (55%), shrub (66%), and desert (51%) landcover types. Probability of use strongly decreased with increasing distance from water (91%). The predictive map developed showed mountain lion use was greater in valley bottoms, along water systems and in closed canopy cover types, decreased at elevations above 3,000 m and slopes greater than 42 degrees. (Figure A1). The predictive map covering the spring 95% MCP home range of female Sierra bighorn sheep in 2016 from the Mt. Langley subpopulation showed considerable variation (0.04–0.78%) in probability of use by mountain lions (Figure A2).

Although I did not explicitly test hypotheses, these results support the assumption that mountain lions are primarily using habitat where mule deer are likely to occur (Johnson et al. 2013) and near closed cover types, where mountain lions have higher chances of ambush hunting success (Dickson and Beier 2002). These findings suggest that slopes ≥ 42 degrees represent locations with low predation risk and can be designated as safe 'escape terrain' for Sierra Nevada bighorn. These results are consistent with my expectations and analogous previous research on the habitat use patterns of mountain lions in high desert-alpine regions, yet are specific to mountain lions within the Sierra Nevada region (Pierce et al. 1999, Ernest et al. 2000, 2002, Dickson and Beier 2002, Stephenson et al. 2012, Johnson et al. 2013, Blake and Gese 2016). The development of this mountain lion RSF and predictive map provides a strong method for determining the relative mountain lion predation risk within SNBS habitat across subpopulations.

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Table B1. Model selection for the top candidate models representing relative probability of use by mountain lions in spring, developed from a resource selection function using GPS data from 28 mountain lions between 2002–2011.

Model	K^a	BIC [b]	ΔBIC[c]	ω[c]	LL[d]
slope quad+ elev quad +full	13	86413.5	0.00	1	-42511.31
slope quad +elev +full	12	86508.8	660.14	0	-43188.8
slope +elev+ rugged +full	12	87842.6	1329.16	0	-43853.3
slope + elev+full	11	88130.1	1616.68	0	-44002.8

[a] *k*= number of parameters, [b]ΔBIC=difference between the model listed and the BIC of the best model [c]*w*= model weight based on model BIC compared to all other BIC values, [d]LL=log-likelihood; slope quad= slope + slope^2, elev quad= elevation + elevation^2, full= full model including: aspect, and distance to vegetation cover types (desert, shrub, riparian, forest, and alpine barren), and distance to streams and seasonal drainages.

Table B2. Standardized regression coefficients and standard errors for the top ranked resource selection function model for mountain lion use in the southcentral portion of the Sierra Nevada, California, USA during 2002–2011.

Model covariate	ß-coefficient	SE
(intercept)	-1.26	0.06
aspect	-0.08	0.03
elevation	-0.39	0.02
elevation^2	-0.36	0.01
slope	0.41	0.01
slope^2	-0.3	0.01
riparian	-0.59	0.02
forest	-0.39	0.03
desert	-0.67	0.06
alpine	0.24	0.01
shrub	-0.41	0.03
water	-0.09	0.01

Figure B1. Spatial maps cover the Southcentral portion of the Sierra Nevada. The predictive map (left) displaying the relative predicted probability of use by mountain lions and was derived from a resource selection function including GPS mountain lion data from 2002–2011. This map indicates mountain lion use is greater in valley bottoms, lower elevations and low-grade slopes. The map on the right displays topographic attributes of the region as well as subpopuilations of Sierra Nevada Bighorn sheep for comparison.

Figure B2. Predictive maps displaying the relative predicted probability of use by mountain lions derived from a resource selection function using GPS location data from mountain lions in the southcentral portion of the Sierra Nevada during 2002–2011. The blue polygon represents the 95% MCP spring home range of Sierra Nevada bighorn sheep from the Mt. Langley subpopulation. There is considerable variation (0.04–0.78%) in probability of use by mountain lions within this home range. The map on the right highlights predefined ‘escape terrain’ for Sierra Nevada bighorn sheep, where the slope is greater than 42 degrees. The relative probability of use by mountain lions in escape terrain is very low.

Figure B1.

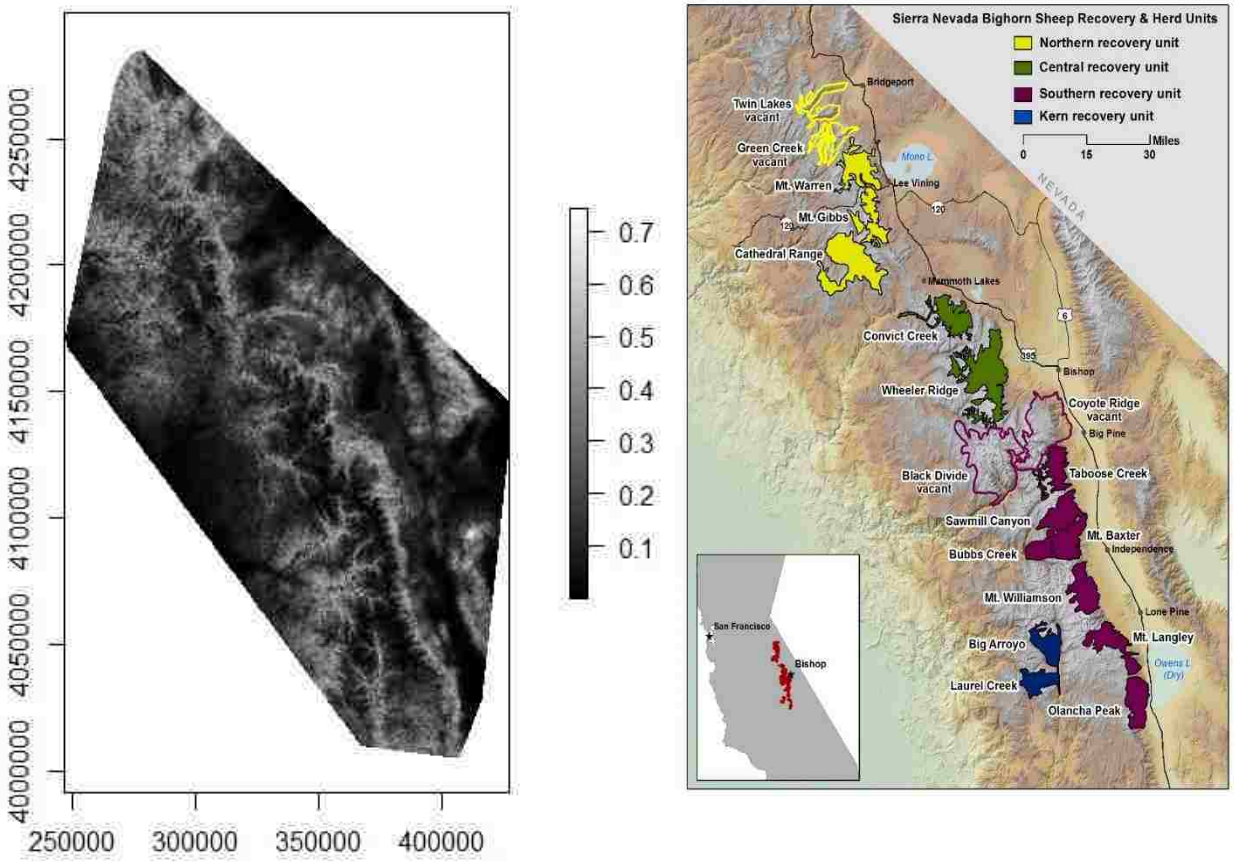
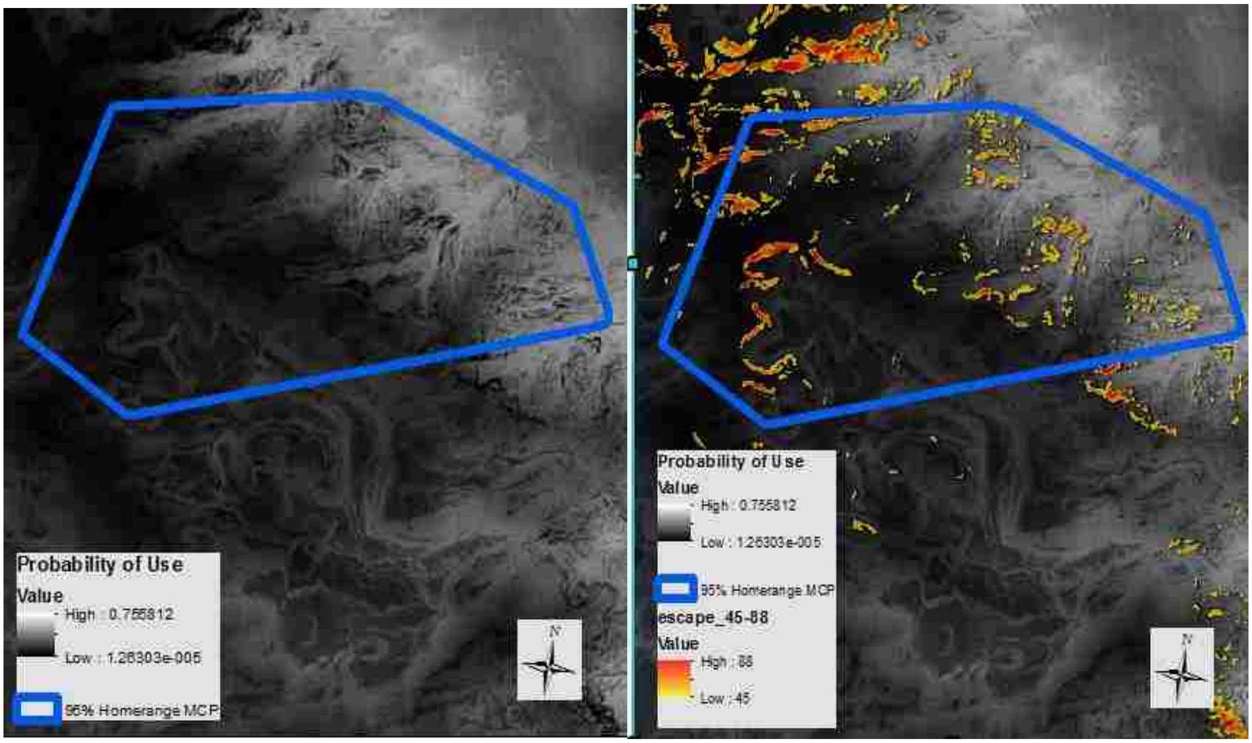

4000000
4050000
4100000
4150000
4200000
4250000
250000
300000
350000
400000
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Sierra Nevada Bighorn Sheep Recovery & Herd Units
Northern recovery unit
Central recovery unit
Southern recovery unit
Kern recovery unit
0
15
30
Miles
NEVADA
Bridgeport
Twin Lakes vacant
Green Creek vacant
Mono L.
Mt. Warren
Lee Vining
120
Mt. Gibbs
120
Cathedral Range
Mammoth Lakes
6
Convict Creek
395
Bishop
Wheeler Ridge
Coyote Ridge vacant
Big Pine
Taboose Creek
Black Divide vacant
Sawmill Canyon
Mt. Baxter
Bubbs Creek
Independence
Mt. Williamson
Lone Pine
Mt. Langley
Big Arroyo
Owens L. (Dry)
Laurel Creek
Olancha Peak
San Francisco
Bishop

Figure B2.


Probability of Use
Value
High : 0.755812
Low : 1.26303e-005
95% Homerange MCP
N
Probability of Use
Value
High : 0.755812
Low : 1.26303e-005
95% Homerange MCP
escape_45-88
Value
High : 88
Low : 45
N

APPENDIX C: PREDICTIVE RESOURCE SELECTION BY SUBPOPULATION

I developed a predictive resource selection funtion to map reource selection by lactating Sierra Nevada bighorn sheep (*Ovis canadensis sierrae;* Sierra bighorn sheep hereafter) in the Sierra Nevada of California. This metapopulation currently consists of 14 subpopulations distributed along the Sierra Nevada crest. One of the potential factors identified by U.S Fish and Wildlife Service (2007) to be limiting recovery includes limited distributions and inadequate connectivity among subpopulations. Despite considerable progress towards recovery, demographic variation among subpopulations remains a threat to recovery (U.S Fish and Wildlife Service 2007, Johnson et al. 2010, Conner et al. 2018). Inter-population connectivity and recolonization of suitable habitat can increase long-term viability for naturally fragmented subpopulations. Sierra bighorn sheep are philopatric and slow to naturally recolonize, thus to achieve recovery goals, managers are focused on reintroductions into former ranges and augmentation of smaller subpopulations (Geist 1971, Few et al. 2015). I used a resources selection function to quantify selection of neonatal habitat by lactating Sierra bighorn sheep, and produce the following maps. The 14 distinct subpopulations are geographically grouped into metapopulation recovery units (Figure C1): Northern recovery unit {Mt. Warren (Figure C2), Mt. Gibbs (Figure C3) and Cathedral Range (Figure C4)}, Central recovery unit {Convict Creek (Figure C5) and Wheeler Ridge (Figure C6) Southern recovery unit {Taboose Creek (Figure C7), Sawmill Canyon (Figure C8), Mt. Baxter (Figure C9), Bubbs Creek (Figure C10), Mt. Williamson (Figure C11), Mt. Langley (Figure C12), and Olancha Peak (Figure C13)}, and Kern recovery unit {Big Arroyo (Figure C14) and Laurel Creek (Figure C15)}. There are currently 4 vacant subpopulations that have been identified by U.S. Fish and Wildlife for future occupancy; Twin Lakes (Figure C16), Green Creek (Figure C17), Coyote Ridge (Figure C18) and Black Divide (Figure C19). The

Black Divide contains the largest proportion of lamb rearing habitat with high and very high probabilities of selection by lactating females. Coyote Ridge contained the smallest proportion of habitat with high and very high probabilities of selection by lactating female.

Figure C1. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep across fourteen occupied and four vacant subpopulations in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C2. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Mt. Warren subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C3. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Mt. Gibbs subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C4. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Cathedral Ridge subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C5. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Convict Creek subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C6. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Wheeler Ridge subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C7. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Taboose Creek subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C8. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Sawmill Ridge subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C9. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Mt. Baxter subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C10. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Bubbs Creek subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C11. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the MT. Williams subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C12. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Mt. Langley subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C13. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Olancha Peak subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C14. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Big Arroyo subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C15. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Mt. Laurel subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C16. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the vacant Twin Creek subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C17. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the vacant Green Lake subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C18. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the vacant Coyote Ridge subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C19. Predictive map displaying the relative predicted probabilities of selection of neonatal lambing habitat by lactating Sierra Nevada Bighorn sheep within the Black Divide subpopulation in the Sierra Nevada of California. This map was developed from 123 animal-years between 2008 and 2017 from a used-available resource selection function. Dark red colors indicate habitat where relative predicted probability of use is highest.

Figure C1.

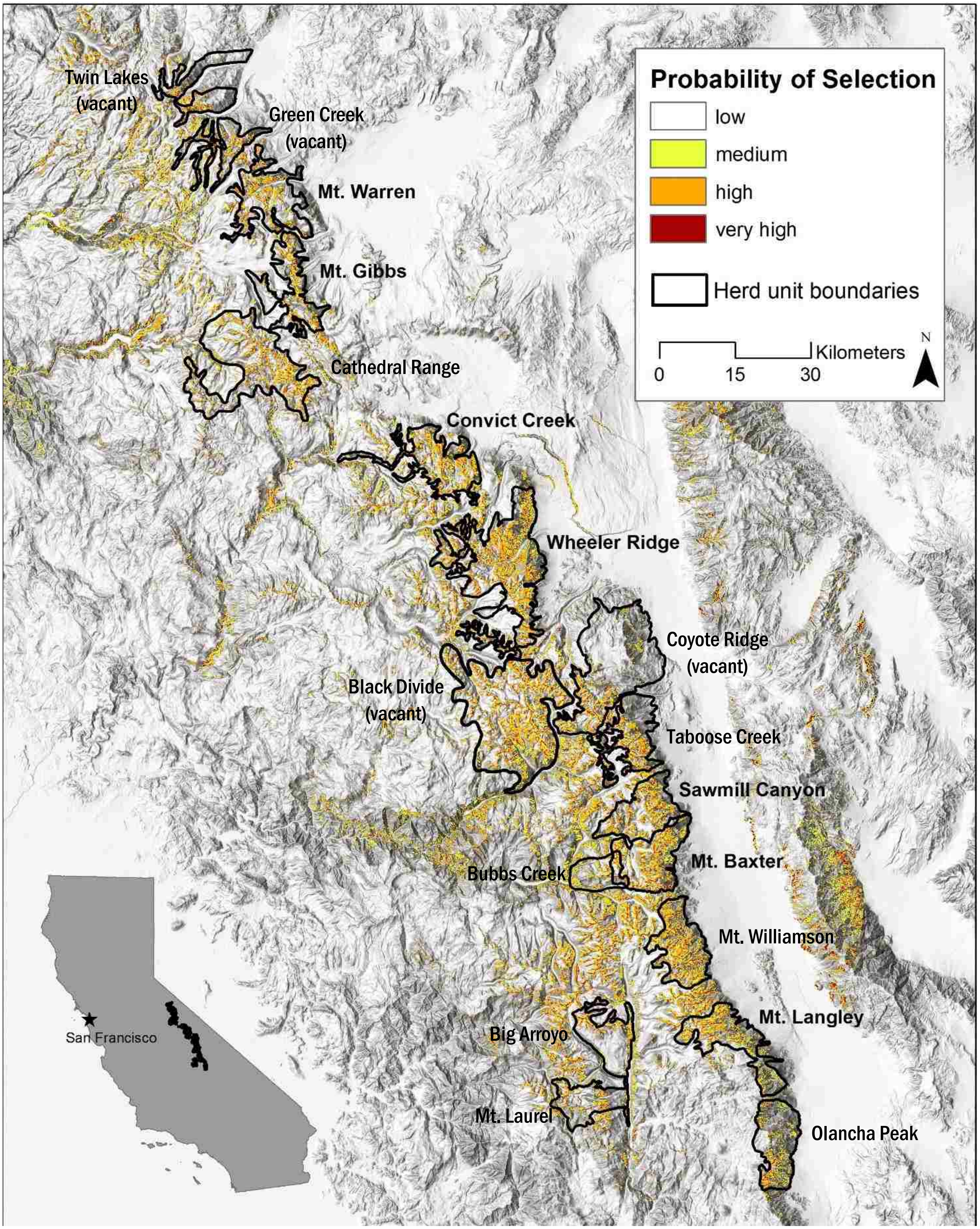

Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
15
30
Kilometers
N
Twin Lakes (vacant)
Green Creek (vacant)
Mt. Warren
Mt. Gibbs
Cathedral Range
Convict Creek
Wheeler Ridge
Coyote Ridge (vacant)
Black Divide (vacant)
Taboose Creek
Sawmill Canyon
Mt. Baxter
Bubbs Creek
Mt. Williamson
Mt. Langley
Big Arroyo
Mt. Laurel
Olancha Peak
San Francisco

Figure C2.

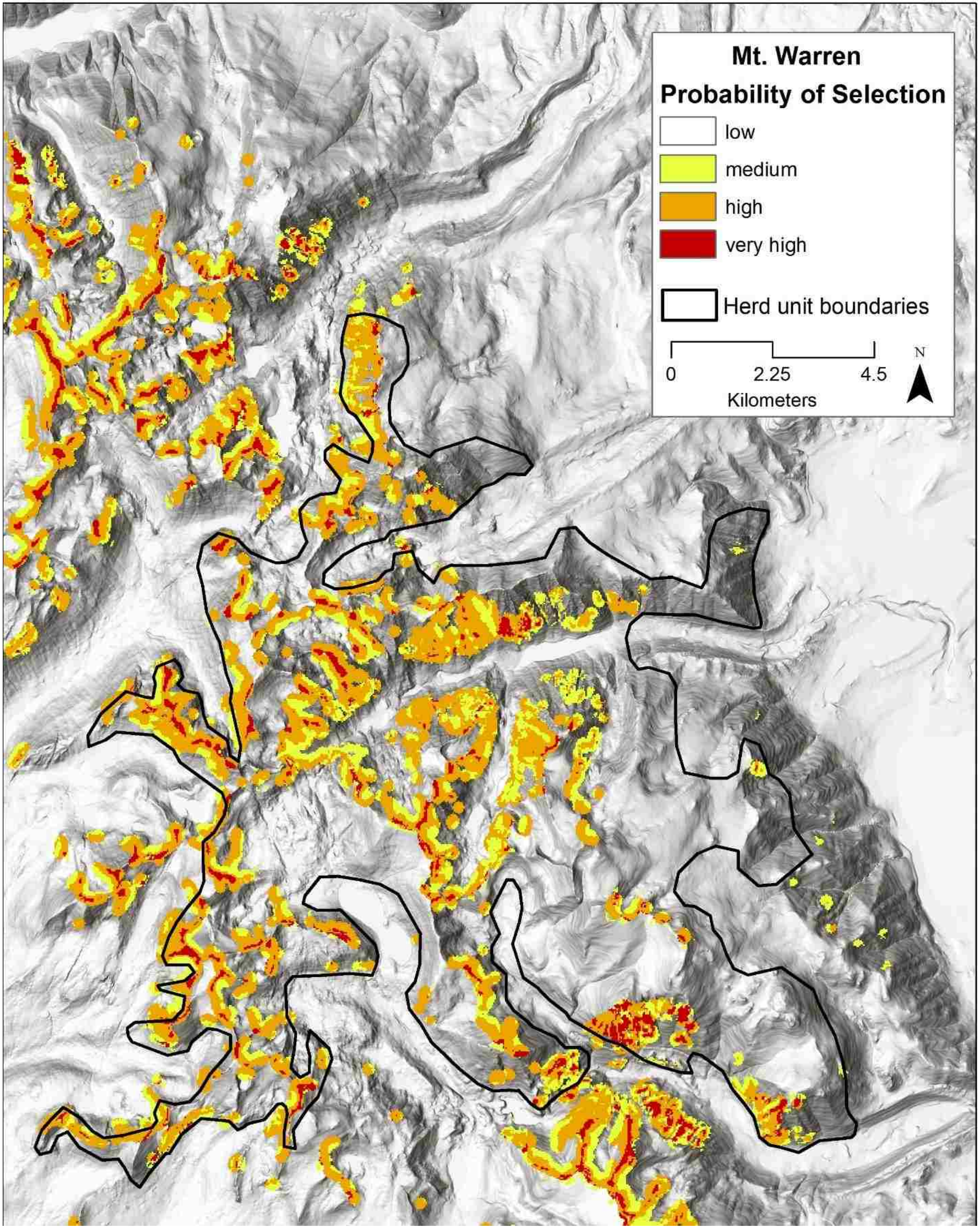

Mt. Warren
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C3.

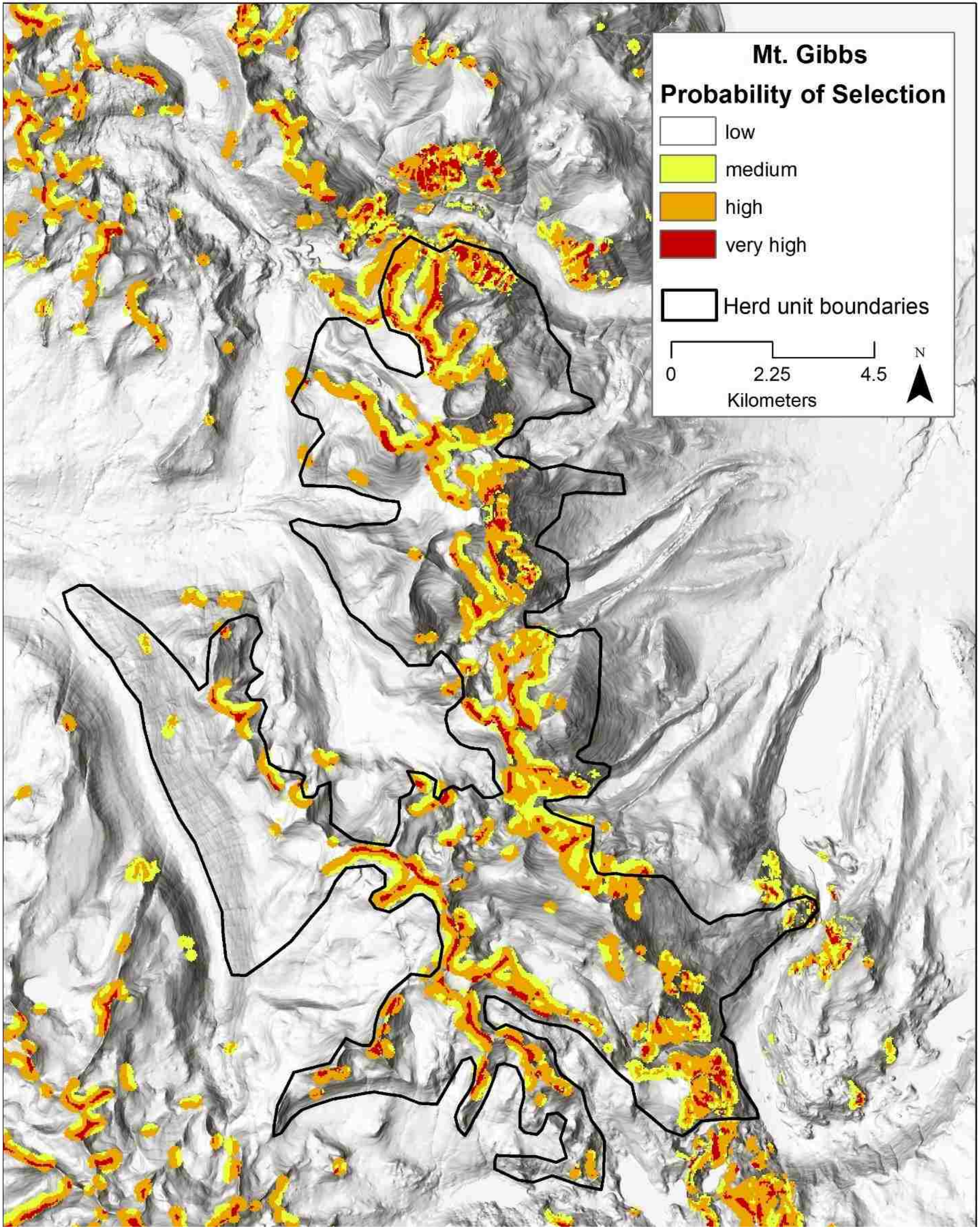

Mt. Gibbs
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C4.

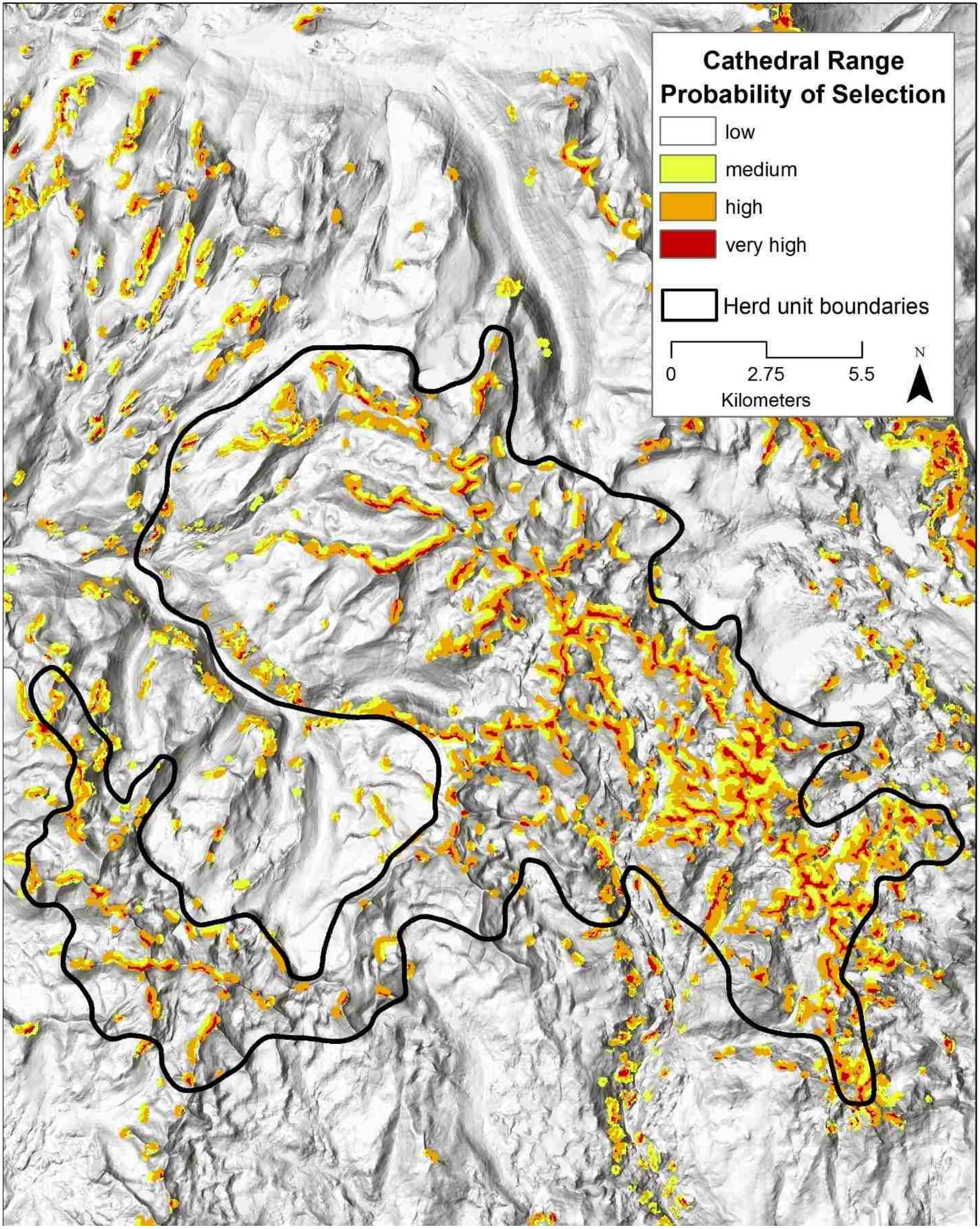

Cathedral Range
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.75
5.5
Kilometers
N

Figure C5.

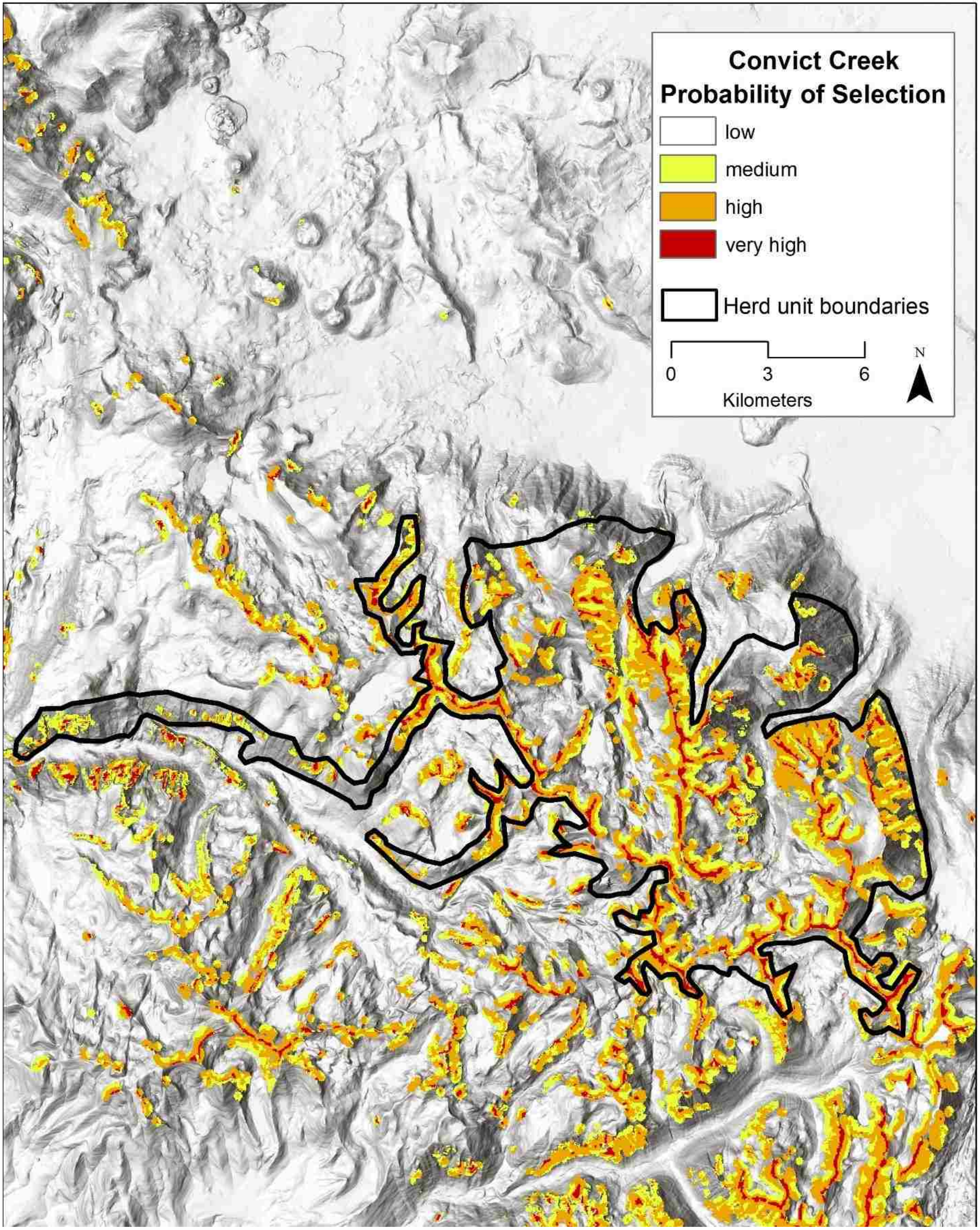

Convict Creek
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
3
6
Kilometers
N

Figure C6.

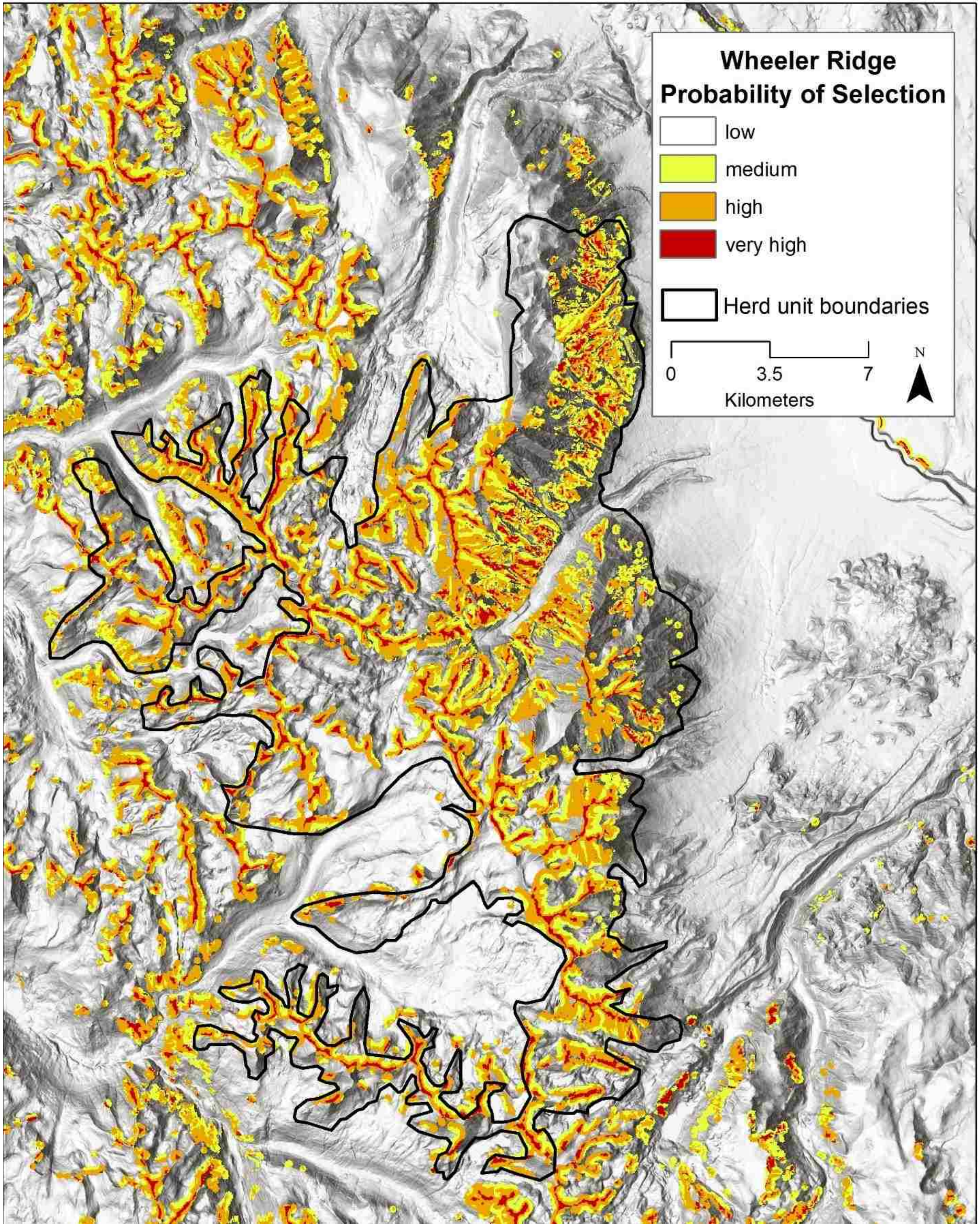

Wheeler Ridge
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
3.5
7
Kilometers
N

Figure C7.

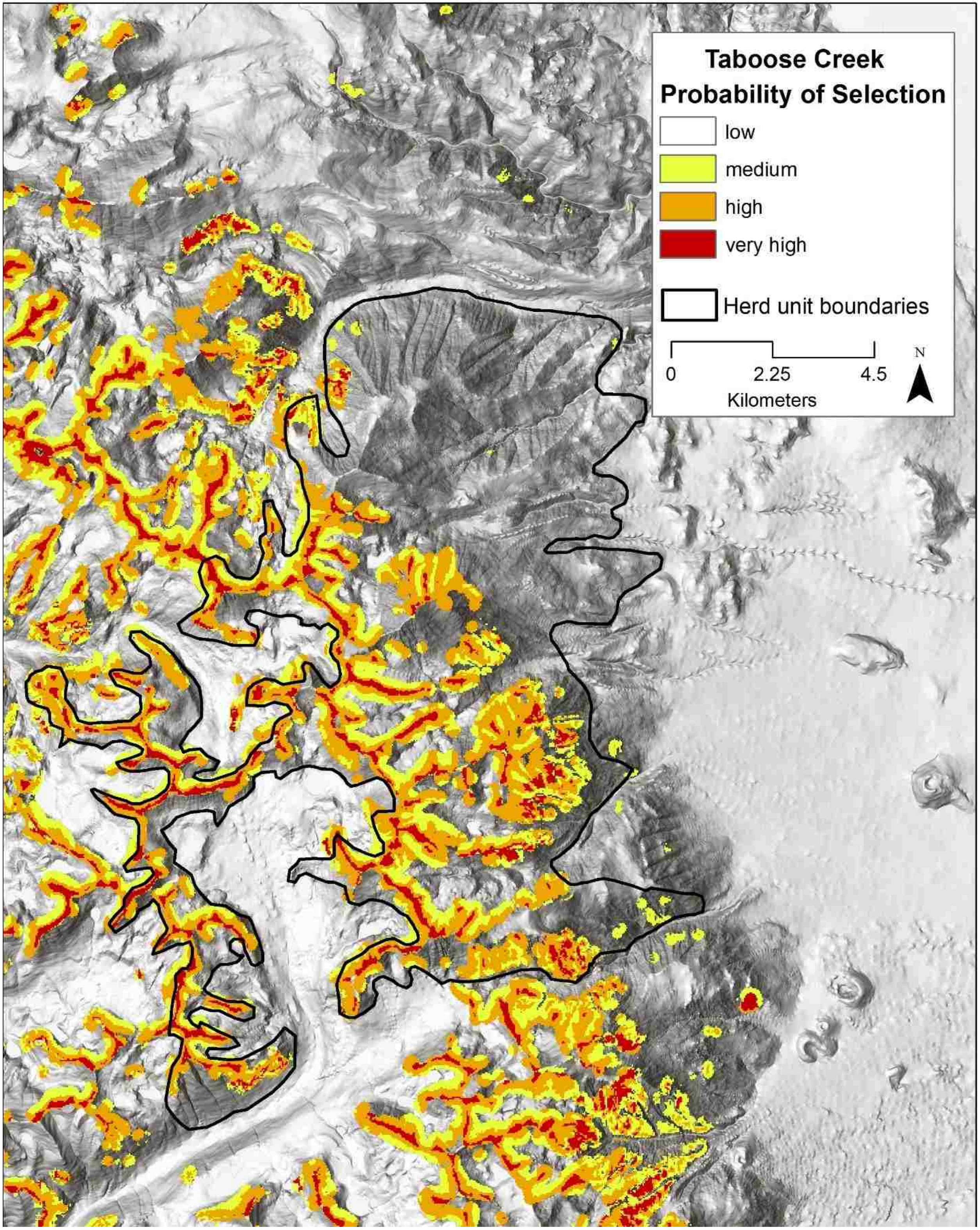

Taboose Creek
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C8.

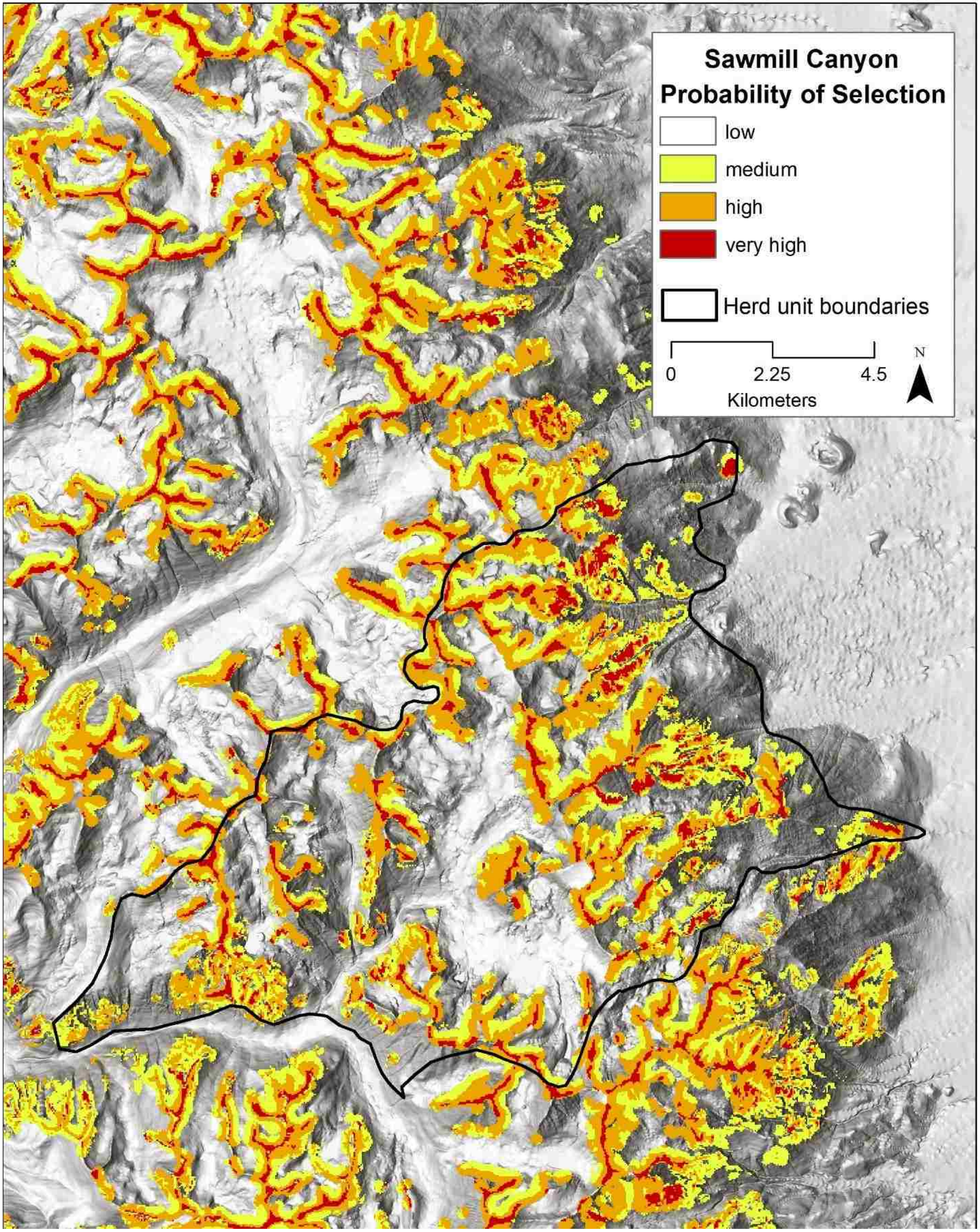

Sawmill Canyon
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C9.

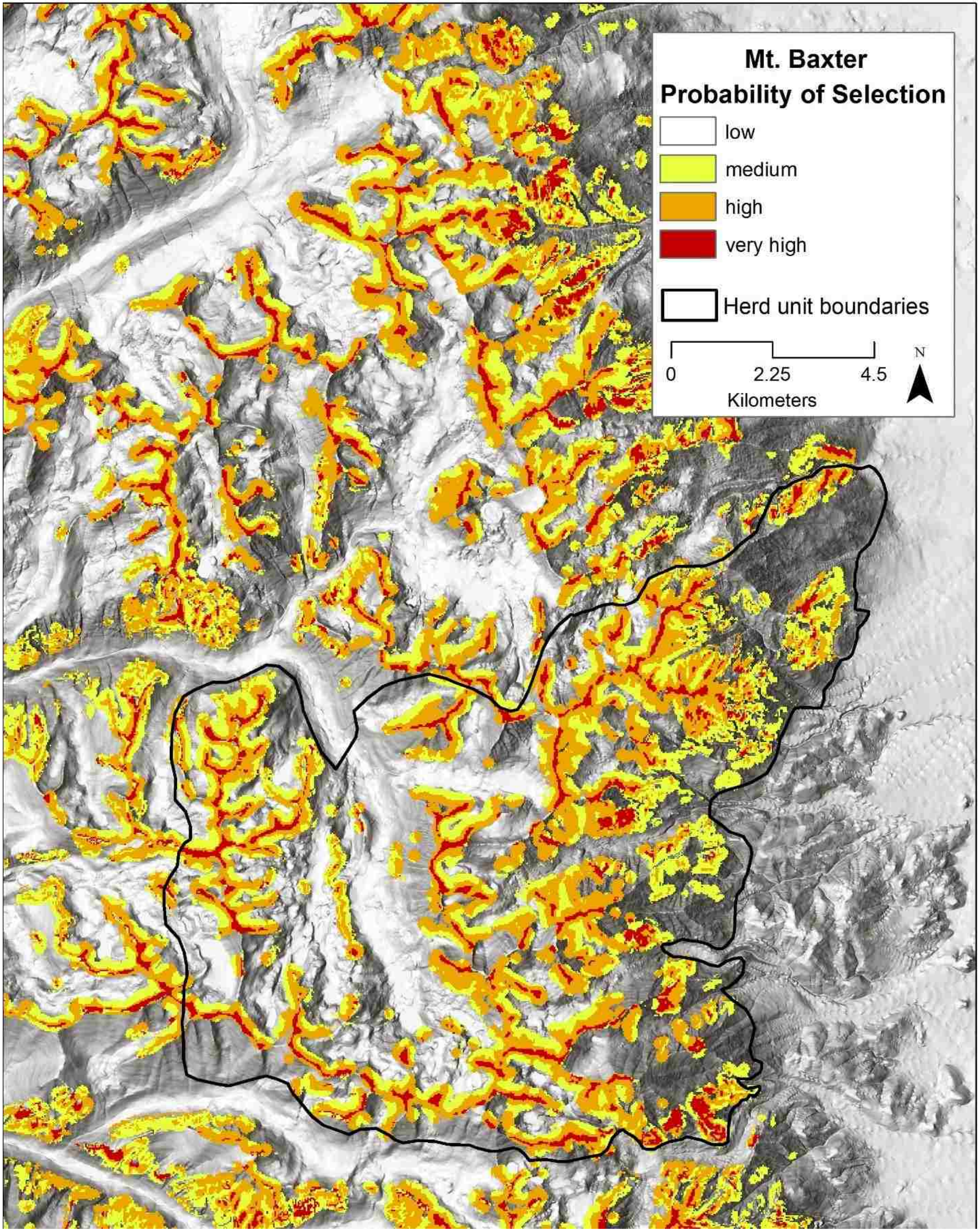

Mt. Baxter
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C10.

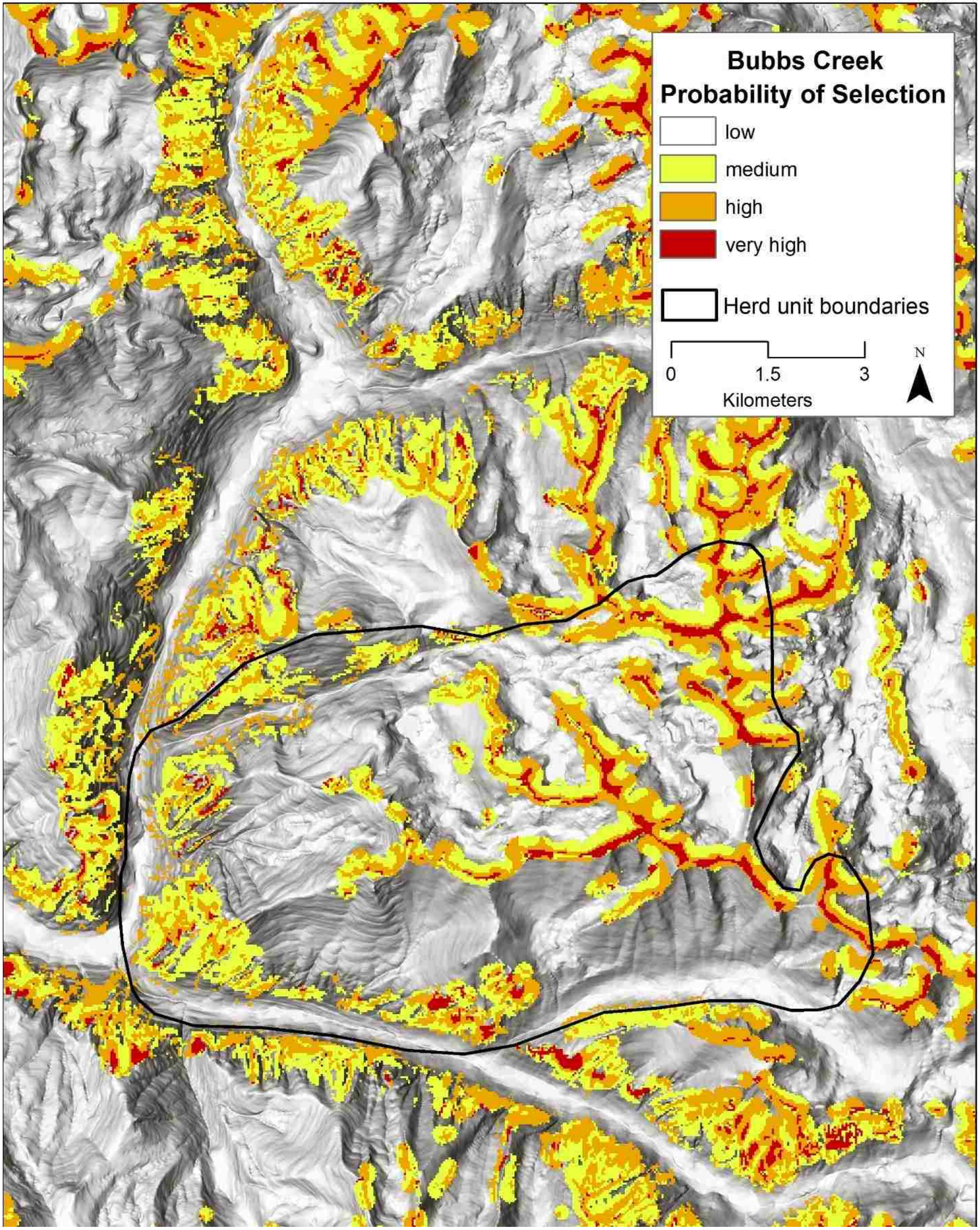

Bubbs Creek
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
1.5
3
Kilometers
N

Figure C11.

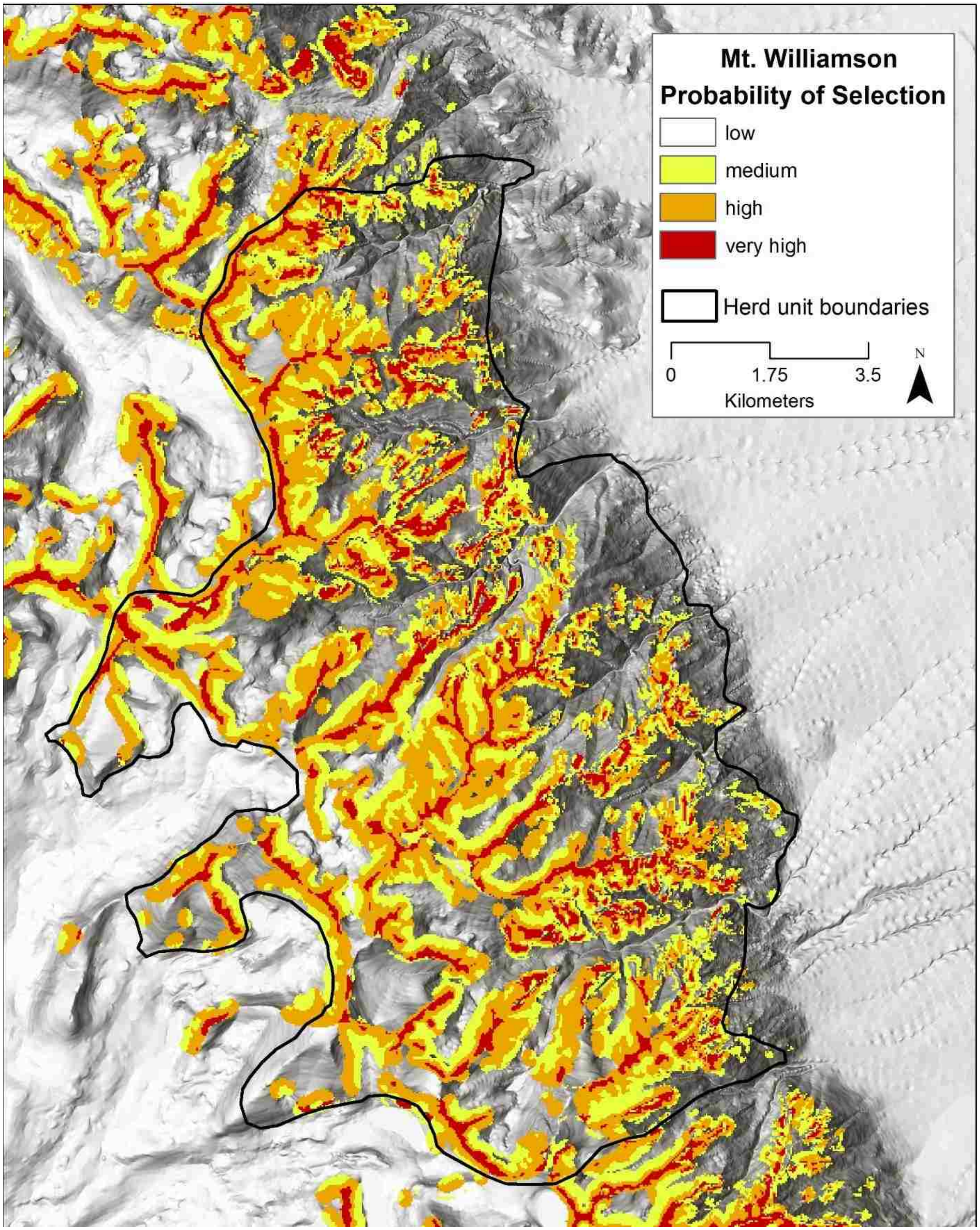

Mt. Williamson
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
1.75
3.5
Kilometers
N

Figure C12.

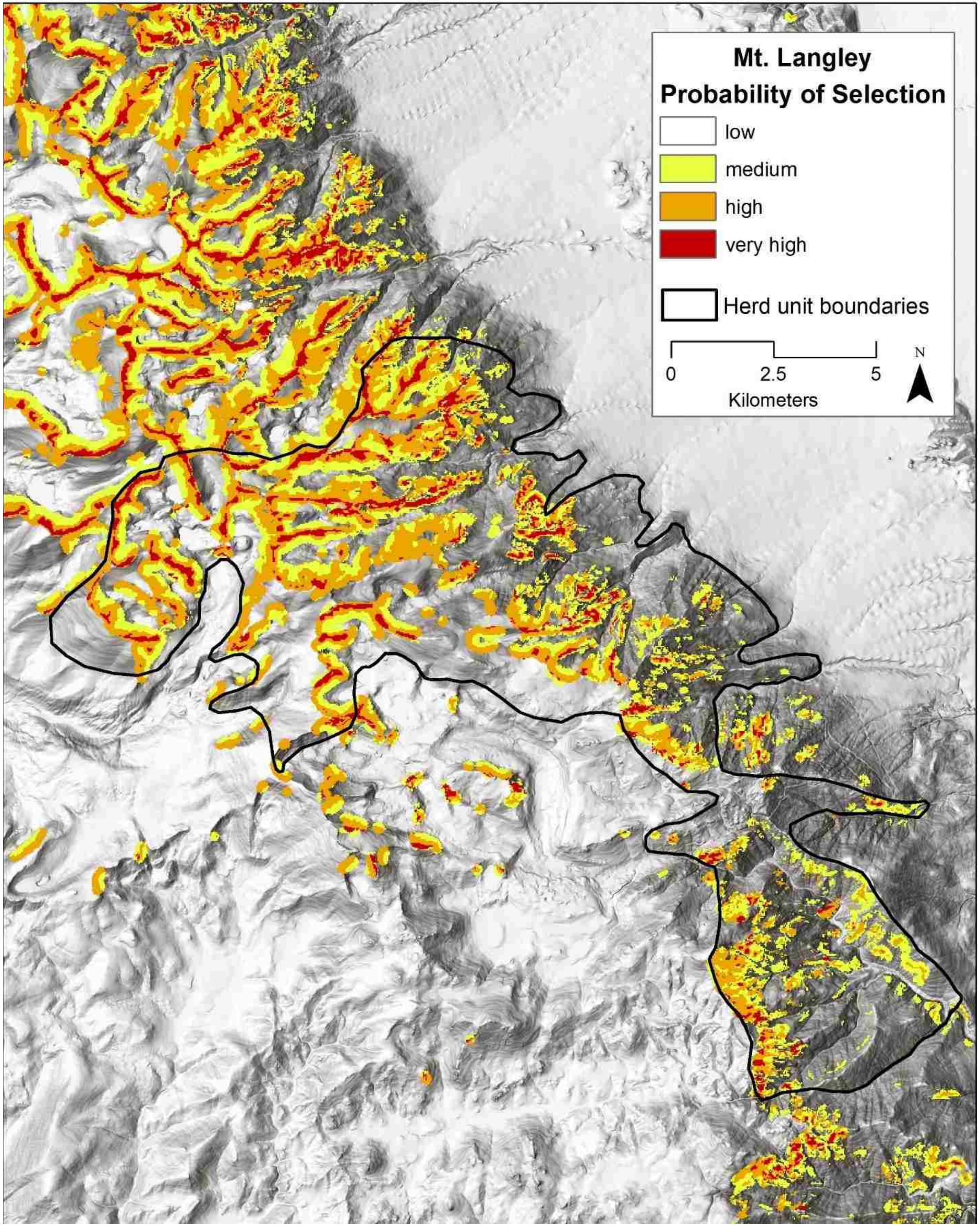

Mt. Langley
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.5
5
Kilometers
N

Figure C13.

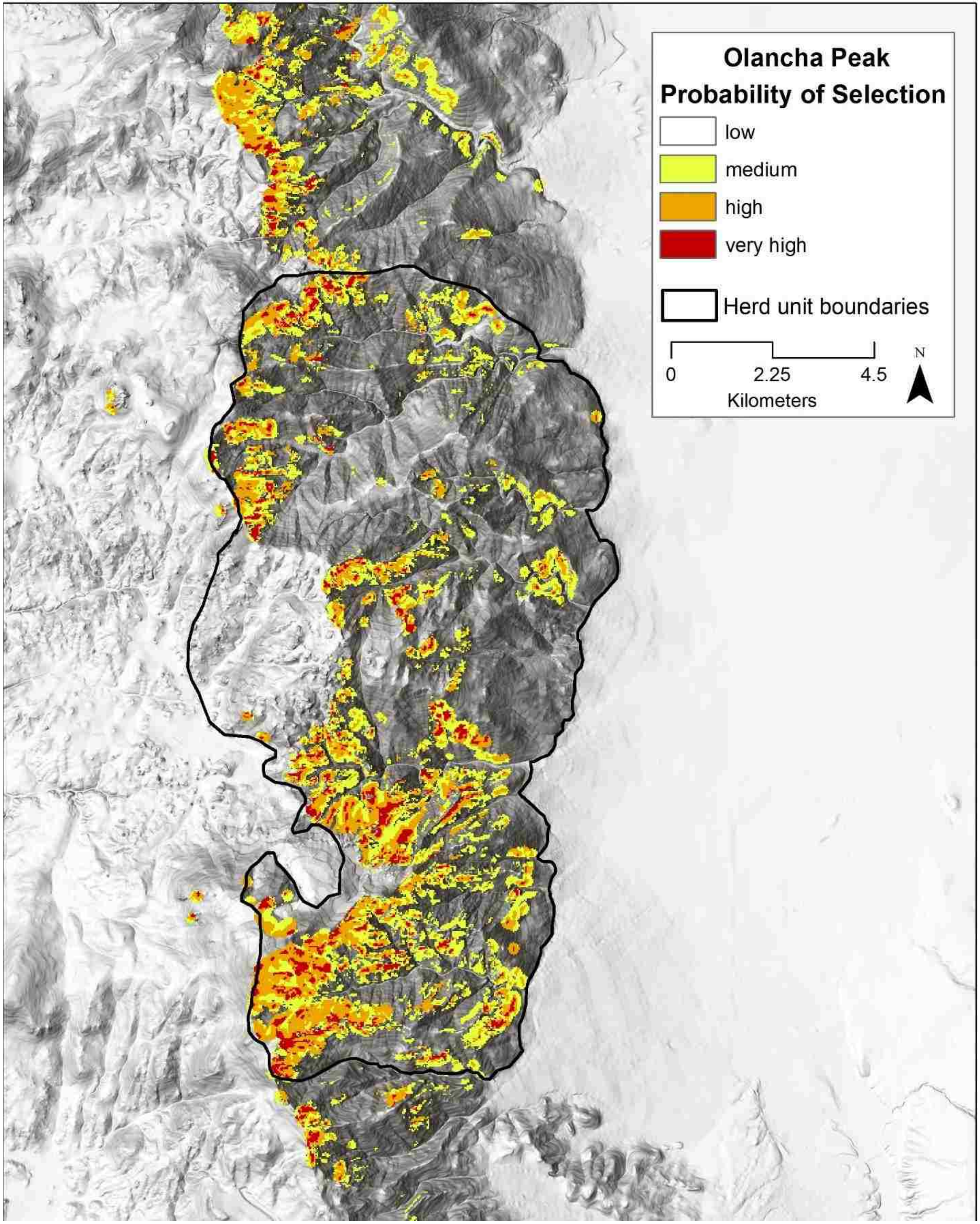

Olancha Peak
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C14.

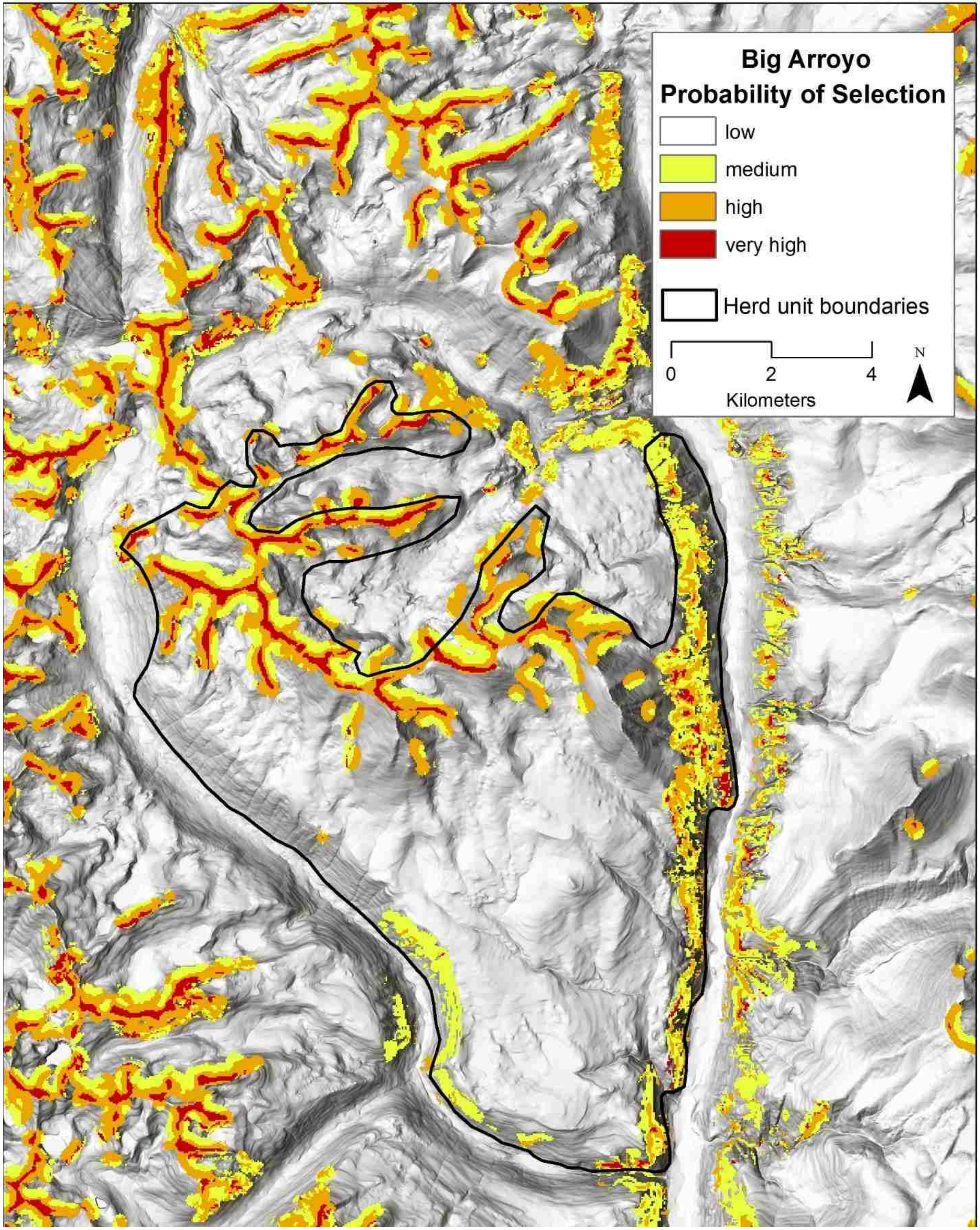

Big Arroyo
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2
4
Kilometers
N

Figure C15.

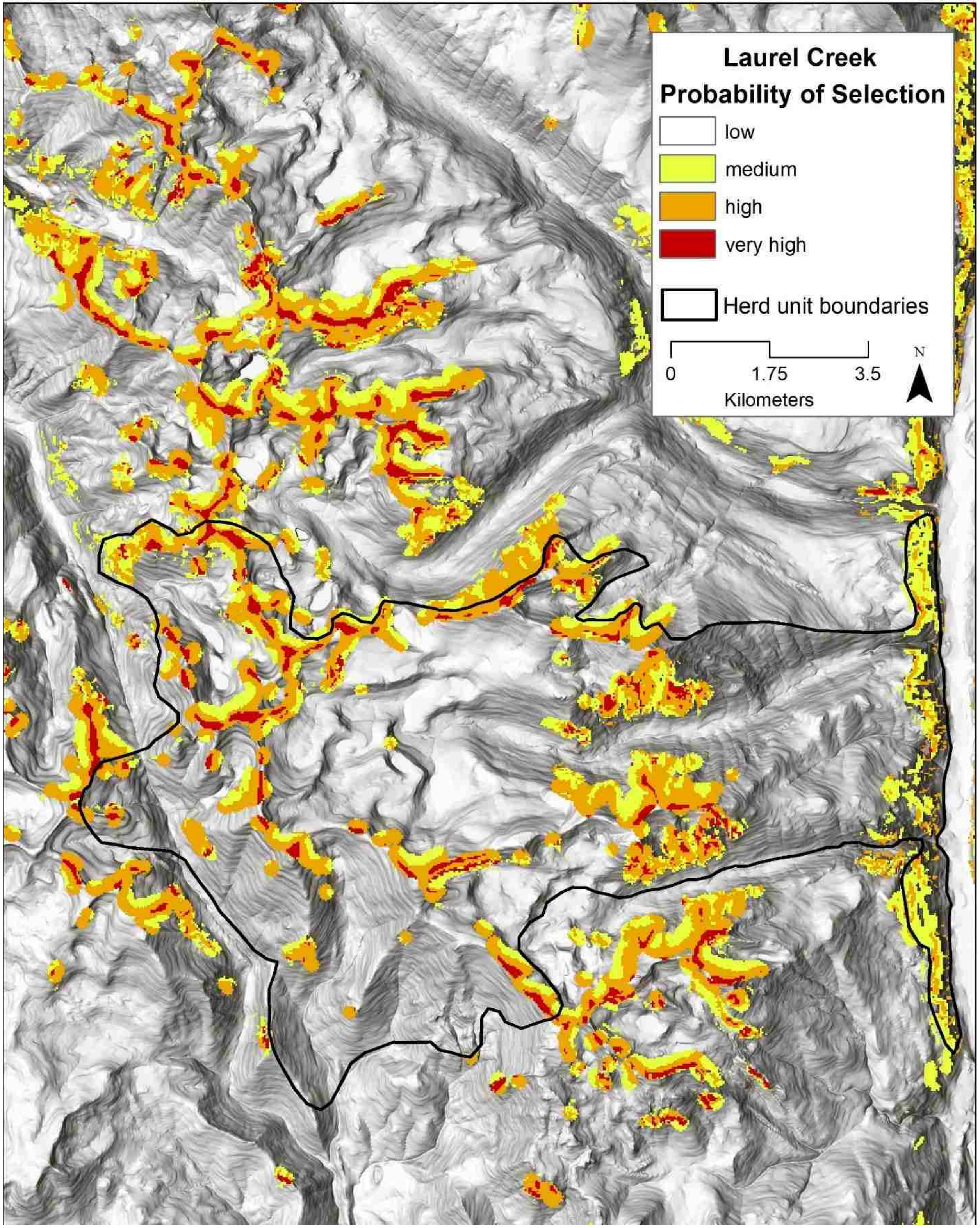

Laurel Creek
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
1.75
3.5
Kilometers
N

Figure C16.

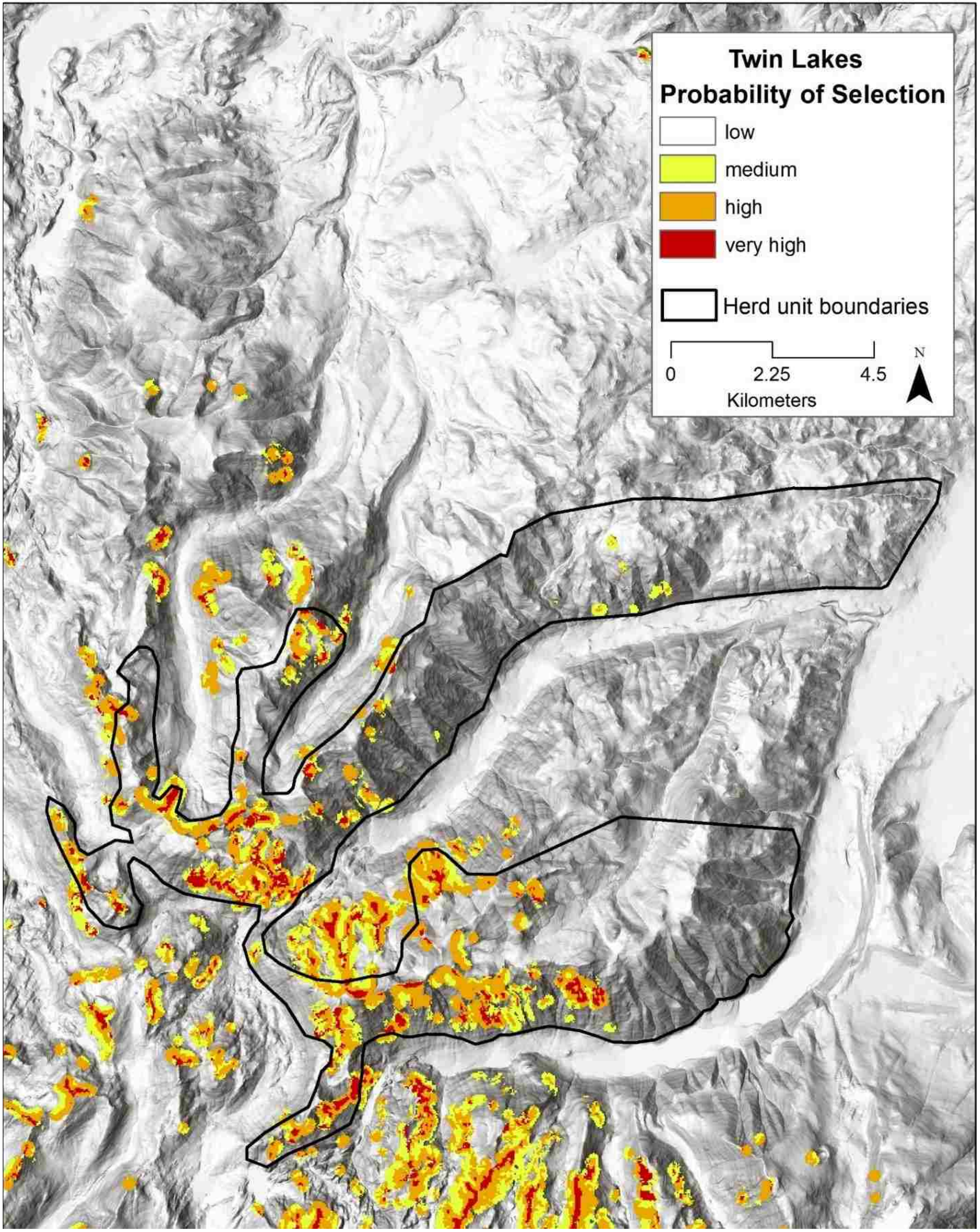

Twin Lakes
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C17.

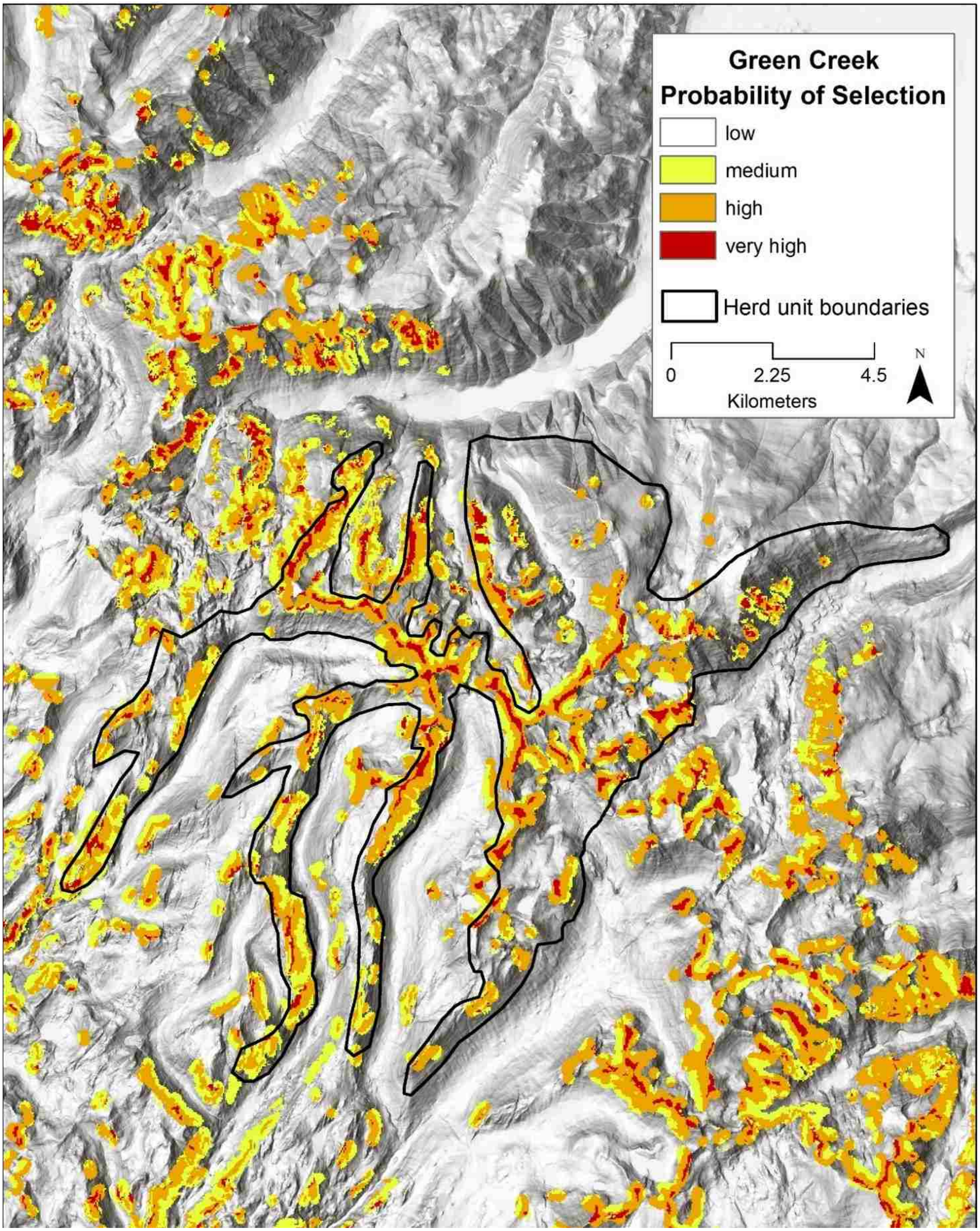

Green Creek
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
2.25
4.5
Kilometers
N

Figure C18.

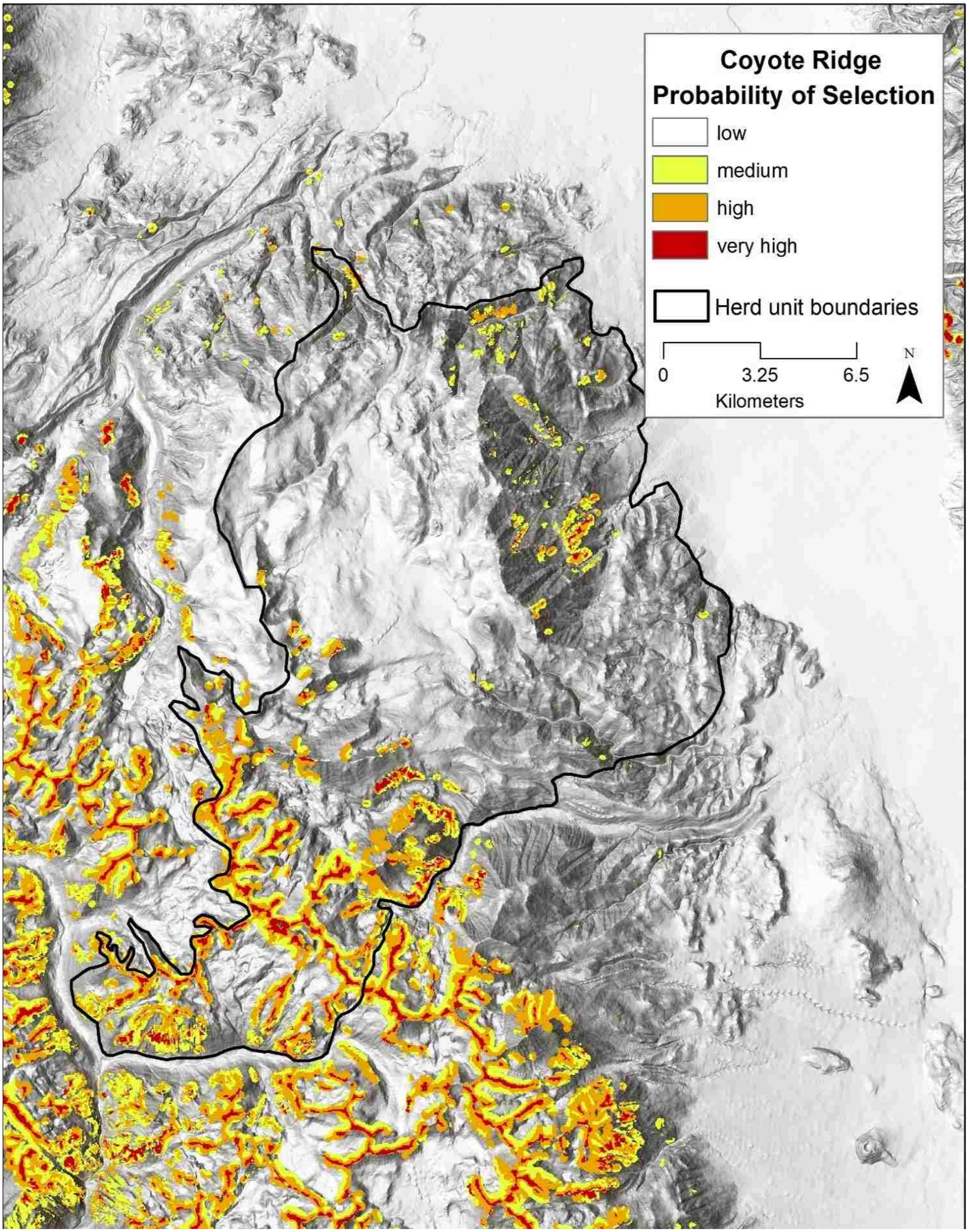
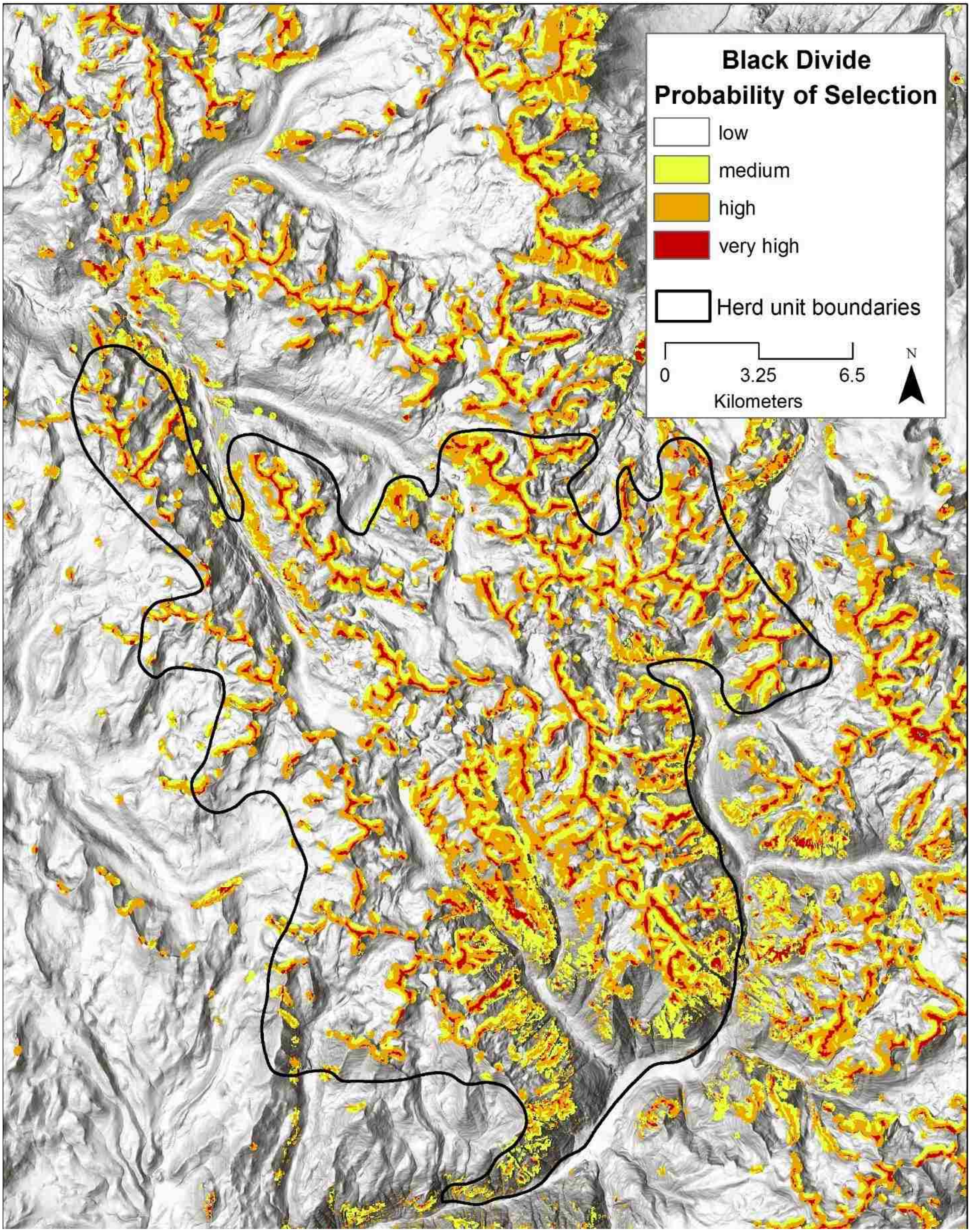

Coyote Ridge
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
3.25
6.5
Kilometers
N

Figure C19.


Black Divide
Probability of Selection
low
medium
high
very high
Herd unit boundaries
0
3.25
6.5
Kilometers
N

CHAPTER 2:
INCREASED EXPOSURE TO RISK OF PREDATION REDUCES NEONATE SURVIVAL IN SIERRA NEVADA BIGHORN SHEEP

ABSTRACT

Populations of bighorn sheep (*Ovis canadensis*) declined rapidly across North America with European settlement in the 1800s (Valdez and Krausman 1999); Sierra Nevada Bighorn sheep (*O. c sierrae*) are today the rarest subspecies of all North American mountain sheep.

Development of effective management strategies for recovering endangered populations requires understanding factors that influence mortality risk for the age-class with the highest potential for improvement. When adult survival is high, mortality of juveniles can be an important driver of population dynamics, but little is known about the causes of Sierra bighorn lamb mortality or characteristics that predispose lambs to mortality. I examined the effects of habitat quality, nutrition, risk of predation, and inbreeding depression on survival of neonatal Sierra bighorn sheep. Overall, 39% of the lambs in our study died during the neonatal period, the majority of the mortalities occurred during the beginning of the lambing season (April), within the first month post-partum, and risk increased when lactating females traveled farther from the safety of escape terrain. I found support for the primary hypothesis that increased exposure to predation is the primary cause of mortality for neonatal Sierra bighorn sheep. Lamb recruitment routinely limits population growth in bighorn sheep, identifying factors affecting survival of neonates can contribute to the development of strategies aimed at improving population dynamics.

My results highlighting the relationship between neonatal lamb survival and habitat characteristics provides guidance as to the likely value of potential habitats within the Sierra Nevada and prospects for recovering bighorn.

KEYWORDS: Sierra Nevada bighorn sheep, neonate, predation, nutrition, inbreeding depression, nest-survival model.

INTRODUCTION

Juvenile recruitment is a key ecological measure that can influence population trajectories, and may be especially important for small populations (Gaillard et al. 1998, Festa-Bianchet et al. 2006). For ungulates, juvenile mortality is often concentrated in the neonatal period (1-90 days postpartum; Festa-Bianchet 1988, Valdez and Krausman 1999, Smith et al. 2014). Quantifying the factors affecting survival of neonates can lead to the development of age-specific management strategies that can improve recruitment (Bergeron et al. 2008, Gilbert et al. 2014, Smith et al. 2015). In populations where disease risk is relatively low, mortality of neonates is often attributed to starvation or predation (Festa-Bianchet 1988, Linell et al. 1995, Valdez and Krausman 1999, Festa-Bianchet et al. 2006). Quality of habitat selected during the neonatal period by female ungulates can also have consequences on fitness and survival of neonates (Rachlow and Bowyer 1994, Pulliam 2000, Bangs et al. 2005, DeCesare et al. 2014). For neonates in small or isolated populations inbreeding depression can have additive and interactive effects on mortality risk of neonates (Slate et al. 2000, Hogg et al. 2006, Cohas et al. 2009). Evaluating the magnitude and potential for interaction of each of these common factors facilitates the development of management strategies that have the greatest potential to improve survival of neonates and overall population trajectories.

Starvation resulting from inadequate nutrition is a leading cause of mortality for neonatal ungulates (Robbins and Robbins 1979, Clutton-Brock et al. 1987, Linell et al. 1995, Martin and Festa-Bianchet 2010). Body condition of females during late gestation and lactation can have strong effect on body mass and subsequent survival of neonates. Neonates born to females in good body condition (high fat reserves) often have greater body mass and higher chances of survival than neonates born to females in poor body condition (Clutton-Brock et al. 1987, Sams et al. 1996, Gaillard et al. 1997, Adams and Dale 1998, Côté and Festa-Bianchet 2001). Females in poor body condition often decrease reproductive investment or abandon neonates altogether to increase their own survival and future reproductive success rather than allocate already depleted resources to offspring that have low chances of survival (Clutton-Brock et al. 1989, Gaillard and Yoccoz 2003, Therrien et al. 2008, Martin and Festa-Bianchet 2010, Monteith et al. 2014). Body condition of lactating females during the fall breeding period can also affect the timing of birth (Côté and Festa-Bianchet 2001). Birthing seasons in highly seasonal environments are synchronous with the narrow window of favorable climactic conditions and phenology of high quality vegetation (Bunnell 1982, Rachlow and Boywer 1994, Parker et al. 2009). Females in good body condition typically conceive earlier than females in poor body condition (Gerhart et al. 1996, Heard et al. 1997, Cook et al. 2004*a,b;* Gustine et al. 2007). Early-born ungulates may benefit from a longer growth period before harsh weather and extended access to fresh forage growth when it is at peak quality (Festa-Bianchet 1988, Côté and M. Festa-Bianchet 2001, Parker et al 2009). Survival can be low for late-born neonates because they are typically born to females in poor body condition and have reduced access to forage of high quality (Mitchell and Lincon 1973, Bunnell 1982, Reimers and Soerumgaard 1983).

Predation is also an important driver of survival for neonatal ungulates (Linnell et al. 1995, Gaillard et al. 1998, Barber-Meyer and Mech 2008, Arthur and Prugh 2010). Vulnerability of neonates to predators often depends on age and mobility of neonates (Scotton 1998, Hamel and Côté 2009), selection of habitat (Hebblewhite and Merrill 2009), and grouping behavior of conspecifics (Ims 1990, Delm 1990, Jenkins and Barten 2005). Neonates are most vulnerable to predators the first few weeks post-partum because their mobility is low and they are less capable of evading predators (Hass 1989, Scotton 1998, Hamel and Côté 2009, Jaques et al. 2015). Risk of predation varies spatially, consequently selection of habitat by lactating females can affect the probability of encountering predators and the likelihood of detecting and evading predators (Risenhoover and Bailey 1985, Hebblewhite and Merrill 2009, DeMars and Boutin 2018). Alpine species can reduce risk of encountering predators by migrating to high elevations, avoiding mild slopes, and selecting habitat near escape terrain (steep rugged cliffs where prey can outmaneuver predators; Geist 1971, Berger 1991, Wehausen 1996, Hamel and Côté 2007, Hebblewhite and Merrill 2009). Vulnerability to predators can also be influenced by group size and behavior of conspecifics (Estes 1976, Frid 1997, Mooring et al. 2004, Rieucau and Martin 2008). Neonates in groups tend to have higher survival because they benefit from increased detection of predators and defense by numerous vigilant lactating females (Bergerud 1974, Estes 1976, Frid 1997, Mooring et al. 2004) and the dilution effect, where probability of individual risk of mortality is decreased with in a larger group (Pulliam and Caraco 1984, Delm 1990, Ims 1990, Hebblewhite and Pletscher 2002). Group size and composition of alpine ungulates are strongly influenced by season and reproductive state of individuals (Risenhoover and Bailey 1985, Rutberg 1987, Childress and Lung 2003). In late spring pre-parturient females remain on winter ranges until they migrate to lambing habitat to give birth (Chapter 1, Spitz et al. In Press, Mysterud 2013). Early-born neonates, whose lactating females are the first migrate to lamb rearing habitat, are less likely to be in a group than those born later, thus may be more vulnerable to predators (Estus 1976, Adams et al. 1995, Mooring et al. 2004, Raithel et al. 2007, Smith et al. 2014).

Quality of habitat selected during the neonatal period by female ungulates can affect the fitness and survival of neonates (Rachlow and Bowyer 1994, Pulliam 2000, Bangs et al. 2005, DeCesare et al. 2014). Habitat quality is a multidimensional measure that encompass aspects of forage quality, risk of predation, and key abiotic habitat resources. Natural selection should favor selection of high quality habitat that maximize fitness and survival of offspring (Festa-Bianchet 1988, DeCesare et al. 2014). Thus, neonates born to females that select poor quality habitat are less likely to survive the neonatal period.

Inbreeding depression resulting from demographic bottlenecks (an event that strongly reduced the size of a population; Li and Roossinck 2004), prolonged isolation can substantially increase risk of morality for neonates (Keller and Waller 2002, Johnson et al 2011, Brommer et al. 2015). Although inbreeding itself is rarely a proximate cause of mortality, neonates born to females with low genetic variation are unlikely to survive because they are generally weaker, have low birth mass, deformities, and compromised immune systems (Ralls 1979, Cohas et al. 2009, Da Silva et al. 2009, Mainguy et al 2009). Furthermore, females with low genetic diversity are likely to be poor care givers and may be unable to adequately provision and protect neonates (Slate et al. 2000, Hogg et al. 2006, Cohas et al. 2009).

For small populations where juvenile recruitment may be a limiting factor in population growth, it’s important evaluate potential factors affecting survival of neonates (Gaillard et al. 1998, Festa-Bianchet et al. 2006). I evaluated how nutrition, risk of predation, quality of habitat selected by lactating females, and inbreeding depression influenced survival of neonatal Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*)**,** a federally endangered subspecies of bighorn sheep. Sierra bighorn sheep are endemic to the Sierra Nevada of eastern California, USA. Populations of bighorn sheep declined rapidly across North America with European settlement in the 1800s (Valdez and Krausman 1999), and today Sierra bighorn sheep are the rarest subspecies of all North American mountain sheep. Historical and current distributions of Sierra bighorn sheep are restricted to alpine habitat found along the central and southern Sierra Nevada (U.S Fish and Wildlife 2007). In 1999, Sierra bighorn sheep were listed as federally endangered, with approximately 125 detected individuals remaining among 3 isolated subpopulations (U.S. Fish and Wildlife Service 2007). Despite considerable progress towards recovery, high spatial and temporal variation in demography across the 14 subpopulations continue to threaten species recovery (U.S Fish and Wildlife Service 2007, Johnson et al. 2010, Conner et al. 2018).

The effects of predation by mountain lions (Johnson et al 2013), forage quality (Greene et al. 2012), disease (Clifford et al. 2009, Cahn et al. 2011), and inbreeding depression (Johnson et al. 2011) have been evaluated for adult Sierra bighorn sheep. Predation by mountain lions has been a leading cause of mortality for adult Sierra bighorn sheep for decades, accounting for approximately 53% of all known Sierra bighorn sheep mortalities (Johnson et al. 2013, Stephenson et al. 2012). No disease-related mortalities (Cahn et al. 2011) or clinical symptoms of disease (Runcie et al. 2014) have been found since the subspecies was listed. Genetic variation of adult Sierra bighorn sheep was found to be among the lowest reported for any wild population of bighorn sheep, yet it did not affect survival of adult females (Johnson et al. 2011). Recent estimates of adult female survival are relatively high and stable (0.78-0.99; Conner et al. 2018). Pregnancy rates are also relatively high and consistent (90-95%), but observed lamb:female ratios are much lower and more variable (21-86%; Greene et al. 2016). Survival of juveniles captured at 6 months to one year old was estimated to be 83% (T. Stephenson, California Department of Fish and Wildlife, unpublished data), indicating that mortality of juveniles primarily occurs during the neonatal period, yet factors influencing neonatal mortality remain poorly understood for this species (Wehausen 1996, Johnson et al. 2010, 2011).

I examined survival of neonates in seven subpopulations of Sierra bighorn sheep (Mt. Gibbs, Mt. Warren, Convict Creek, Wheeler Ridge, Mt. Baxter, Sawmill Canyon, and Mt. Langley) that represent >85% of the subspecies. My objective was to evaluate whether nutrition, risk of predation, or habitat quality had the greatest effect on survival of neonates, and whether inbreeding depression had additive negative effects. I hypothesized that inadequate nutrition would have the strongest effect on survival of neonates. I then hypothesized that neonates born to females in poor body condition and those born later during the birthing season would suffer from inadequate nutrition and predicted they would have the lowest survival. I alternatively hypothesized that predation would have the greatest effects on the survival of neonates. I then hypothesized that neonates would be most vulnerable to predators during the first few weeks post-partum, if they were born early during the birthing season, and when lactating females selected habitat where the risk of encountering a predator was high and likelihood of evasion was low. Therefore, I predicted that survival would be lowest for neonates less than one month old, neonates born before the peak birth pulse, and neonates born to females that selected habitat where probability of encountering ambush predators was high or habitat that was far from escape terrain. I alternatively hypothesized that the quality of habitat selected by lactating females would have the strongest effects on survival of neonates. I predicted that neonates born to females that selected poor quality habitat during the neonatal period would have the lowest survival. I hypothesized that in addition to hypothesized primary sources of mortality, inbreeding depression would have additive negative effects of survival on neonates. If true, I predicted that neonates born to females with low genetic variation would have lower survival than those born to females with higher genetic variation.

STUDY AREA

The Sierra Nevada extends 650 km along the eastern border of California (Hill 1975). Elevation changes abruptly along the eastern escarpment from 1000 m to an average of 3,000 m, with numerous peaks above 4,000 m. The strong rain shadow effect limits summer (May-September) precipitation east of the Sierra crest, resulting in most of the annual precipitation falling as snow during winter months (November-April). The resulting xeric vegetation communities are separated by elevational gradients; low-elevation communities (1500-2499 m) includes scrub with mixed grass and forb types; intermediate (2500-3300 m) includes moderate timber cover with sparse forbs and subalpine meadows; high elevations (>3300 m) includes sparse alpine vegetation (Hill 1975). Common fauna includes mule deer (*Odocoileus hemionus*), mountain lion (*Puma concolor),* bobcat *(Lynx rufus),* black bear *(Ursus americanus),* coyote *(Canis latrans),* and golden eagle *(Aquila chrysaetos).*

METHODS

Survival Monitoring— California Department of Fish and Wildlife crews captured adult female Sierra bighorn sheep across seven subpopulations from 2008- 2017 using helicopter net-gun methods (University of Montana IACUC 012-16MMMCWRU-022916, Federal Fish and Wildlife Service Permit No. TE050122-4) as a part of a long-term monitoring effort for recovery. We fitted all captured females with global positioning system (GPS) collars, and a sub-sample of pregnant females with vaginal implant transmitters (VIT) and high fix rate collars (12 fixes/day) during 2016–2017 (Bishop et al. 2007).

I determined survival of neonates through the neonatal period (90 days post-partum) by monitoring the presence of neonates-at-heel for select GPS-collared females. I identified parturition for each female using my previously developed cluster detection algorithm (Chapter 1, DeMars et al. 2013, McClintock et al. 2012, 2014, Blackwell et al. 2016). I then calculated the probability of detecting a lamb known to be present using mark-resight estimation based on the presence of lamb-at-heel for marked females by surveying spring lamb ranges during the early neonatal lambing period (Bonenfant et al. 2005). Given that twinning has not been observed in Sierra bighorn and females do not allow non-related offspring to suckle, lamb presence could be assessed accurately from visual observations. I made multiple attempts to confirm the presence of a lamb for each female, and to resight pairs post-partum on a bi-weekly basis beginning April 1st and continuing through September 30th each spring using binoculars and spotting scopes. Logistical constraints, however, affected the frequency and duration of monitoring. Subpopulations are remote, during spring and summer months Sierra bighorn sheep primarily inhabit elevations above 3,200m, and select for steep rugged terrain that is often difficult to access. Unpredictable weather patterns coupled with dangerous terrain often limited my ability to locate pairs. I ensured, however, that each pair had ≥ 2 observations during the study period. I estimated the probability of sighting/resighting a lamb for each occasion a female was observed post-partum during the early neonatal period.Following the results of this analysis I selected a nest-survival model because our re-capture rate of marked females was very high, thus the assumptions of a known-fate model were adequately met.

Factors Influencing Survival — I evaluated the effects of nutrition on survival of neonates using female body condition (ingesta-free body fat; IFBFat). I estimated percent IFBFat for each female during autumn captures using ultrasonography (Stephenson et al. 1998, Gustine et al. 2007). Next, I evaluated the effects of relative timing of birth by determining parturition for each neonate using a cluster algorithm (Chapter 1). I summarized the distribution of birth dates and defined peak birthing period as the date range that included at least 75% of births. Neonates born before the peak were considered early-born and neonates born after the peak were considered late-born. I considered early-born neonates to be at higher risk of mortality from predation, and late-born to be at higher risk of mortality from decreased access to high quality forage.

Next, I used my previously developed third-order (within home range) level resource selection function developed from the same study area at the same time to estimate spatial variation in habitat quality (Chapter 1, DeCesare 2012). This model integrated probabilities of selection across spatial risk of predation by mountain lions, distance to escape terrain (slope > 42°), vegetation type, terrain ruggedness, and aspect into a single measure of habitat quality (Manly et al. 2002). I then independently assessed how spatial predation risk (probability of encountering a hunting mountain lion) derived from a resource selection function (RSF; Chapter 1) affects survival of neonates by extracting the average likelihood of encounter selected by lactating females during each occasion (Lima and Dill 1990, Hebblewhite et al. 2005, Hebblewhite and Merrill 2009). I also evaluated spatial predation risk by determining the relative probability of evading predators by measuring the average distance to escape terrain (slopes >42°) selected by lactating females during each occasion. Finally, I evaluated the effects of inbreeding depression on survival of neonates using percent heterozygosity of lactating females. I extracted DNA from blood samples taken at captures and used polymerase chain reactions to amplify dinucleotide microsatellite markers and to genotype each individual female following methods described by Johnson et al. (2011). I genotyped 47 microsatellite loci known to be polymorphic in *Ovis* species (Sausman 1984, Overall et al. 2005) and calculated multilocus heterozygosity of each individual female (Mitton 1993, Slate and Pemberton 2002, Mainguy et al 2009). I repeated this procedure to obtain duplicate samples and improve genotyping accuracy. I removed loci that appeared to be monomorphic across subpopulations. I considered multilocus heterozygosity to be a strong measure of genetic variation and an indicator of inbreeding depression (Coltman and Slate 2003, Da Silva et al. 2009, Johnson et al. 2011, Brommer et al. 2015).

I extracted time-sensitive habitat covariates (habitat quality, risk of encounter, distance to escape terrain) selected by each female across the neonatal period then calculated the minimum, maximum and averaged values for each of the six 14-day encounter occasions. This method ensures that survival probabilities for each interval correspond to the time each habitat covariate was selected by lactating females. I then summarized the distribution of each factor across lactating females to quantify the variation within my sample (Dinsmore and Dinsmore 2007). ProgramMARK standardized each variable internally so that the magnitude of each variable was comparable across models (Bring 1994). I considered standardized β-coefficients with confidence intervals that did not overlap 0, and defined coefficients ≤ 0.1 to have weak effects on selection, values $\geq |0.1|$ and ≤ 0.5 moderate, values $\geq |0.5|$ and $\leq |1.0|$ strong, and values $\geq |1.0|$ to have very strong effects (Bring 1994).

Survival Modeling— I evaluated my hypotheses using nest-survival analysis with a logit-link function (Dinsmore et al. 2002, Rotella et al. 2004, Shaffer and Thompson 2007 in Program MARK (Version 8.1, White 2005; White and Burnham 1999). Nest-survival models are considered known-fate models, thus before selecting this model structure I calculated the probability of detecting a lamb known present using mark-resight estimation (Bonenfant et al.

2005). I estimated survival bi-weekly because my data was not robust enough to estimate daily survival (Johnson et al. 2004, Fieberg and DelGiudice 2008, Grovenburg et al. 2014). I considered neonates that survived 90 days (6 bi-weekly occasions) to have survived the neonatal period (Griffin et al. 2011). I binned observations into bi-weekly encounter occasions (Fieberg and Delgudice 2009); occasion 1: early April (April 1st–15th), occasion 2: late April (April 16th–30th), occasion 3: early May (May 1st– 15th), occasion 4: late May (May 16th- 31st), occasion 5: early June (June 1st– 15th), occasion 6: late June (June 16th–30th), occasion 7: early July (July 1st – 15th), occasion 8: late July (July 16th–31st) , occasion 9: early August (August 1st–August 15th), occasion 10: late August (August 16th–30th), occasion 11: early September (September 1st– 15th), occasion 12: late September (September 16th– 30th). I staggered entry into the model based on parturition date. I recorded "Last Present" as the last date a neonate was last observed with a female, and date "Last Checked" as the final occasion that each neonate:female pair was observed during the study period or the 6th occasion for neonates that survived the neonatal period.

I constructed models based on *a priori* hypotheses and evaluated which model(s) best explained survival of neonates. I included a model with year to account for variation among years that I did not specifically address with other covariates such as weather. I included a model with individual subpopulations to account for variation among groups not specifically addressed with other covariates, such as predator distributions, differences in resource availability, and differences in size of subpopulations. I modeled survival in 2 stages. First, I subset the data to include only individuals I had measures of IFBFat for the neonate-year I was modeling. I built a total of 28 models to evaluate my hypotheses; 14 models included combinations of factors I hypothesized would influence nutrition (6 models), risk of predation (7 models), and a single model for overall habitat quality. I included those same 15 models again, each with an additive term to evaluate the effect of inbreeding depression (Table 1). I additionally included a model with year and one with subpopulation to evaluate if variation in survival could be explained by these parameters. I ranked those 15 top models according to Bayesian Information Criteria (BIC Schwartz 1978, Hooten and Hobbs 2015), ΔBIC, and model weight (ωi). I considered models with ≤ 2 ΔBIC values competitive (Burnham and Anderson 2002). I evaluated strength of evidence for factors hypothesized to affect survival based on ΔBIC_c and 95 % confidence intervals (CI) of estimates. Second, I repeated the model building and selection process using all individuals but did not include models with IFBFat. Following the results from both stages of modeling, I selected the final top model based on BIC ranking, 95% CI, and considered this model to best explain survival of neonates.

Following the identification of the top model, I calculated the probability of survival between each encounter occasion, estimated mean survival for lambs by date of birth, and how survival varied across covariates. I estimated model fit by plotting the observed survival outcomes and predicted probabilities because there is currently no goodness-of-fit test available for nest survival models of small sample sizes (Dinsmore et al. 2002, Dinsmore and Dinsmore 2007, Shaffer and Thompson 2007).

RESULTS

Survival Monitoring — I collected 594 observations from 125 neonates from April 1st to September 30th for 2006-2017. A total of 76 (61%) neonates survived the neonatal period and 51 died. I estimated the probability of sighting/resighting a lamb as 0.92 (SE=0.03, n=36 known present lambs) for each occasion a female was observed. I made an average of 5.38 observations per female during the 90 day period, and only included data from females with ≥ 2 observations, thus on average there was <1% chance in missing a lamb. I monitored 38 neonates in the Northern recovery unit (Mt. Gibbs [n=16], Mt. Warren [n=22]), 34 neonates in the Central recovery unit (Convict Creek [n=12], Wheeler Ridge [n=22]), and 53 neonates in the Southern Recovery unit (Mt. Langley [n=27], Mt. Baxter [n=13], and Sawmill Canyon [n=13]).

Factors Influencing Survival — Parturition dates followed a relatively normal distribution (Figure 2); the earliest neonate was born on April 1st and the last on July 10th ($\bar{\chi}$ = May 10th, SD=18 days). I considered the peak birthing period as the 2–4th encounter occasions (April 15th–May 30th) because they contained 97 of the 125 births (78%). Mean IFBFat of lactating females in fall was ($\bar{\chi}$ = 14.2 %, SD= 4.9). Lactating heterozygosity was calculated from 42 polymorphic loci was ($\bar{\chi}$ = 50.3 %, SD=8.7). Lactating females selected habitat with quality measures on average that were ($\bar{\chi}$ = 71.3%, SD = 0.05) during the first occasion post-partum, ($\bar{\chi}$ = 67.2% , SD = 0.05) during the second, ($\bar{\chi}$ = 65.7% m , SD = 0.04) during the third, ($\bar{\chi}$ = 63.6% m , SD = 0.04) during the fourth, ($\bar{\chi}$ = 60.3% m , SD = 70.1) during the fifth, and ($\bar{\chi}$ = 58.4% m , SD = 0.05) during the final occasion. On average, lactating females selected for distances to escape terrain that were ($\bar{\chi}$ = 66.4 m , SD = 40.5) during the first occasion post-partum, distances that were ($\bar{\chi}$ = 79.0 m , SD = 50.8) during the second, ($\bar{\chi}$ = 87.6 m , SD = 44.7) during the third, ($\bar{\chi}$ = 100.2 m , SD = 53.0) during the fourth, ($\bar{\chi}$ = 120.3 m , SD = 70.1) during the fifth, and ($\bar{\chi}$ = 130.8 m , SD = 66.3) during the final occasion. The average probability of encountering hunting mountain lion was ($\bar{\chi}$ = 8% , SD = 0.5) during the first occasion post-partum, distances that were ($\bar{\chi}$ = 7% , SD = 0.3) during the second, ($\bar{\chi}$ = 8% , SD = 0.3) during the third, ($\bar{\chi}$ = 9% , SD = 0.5) during the fourth, ($\bar{\chi}$ = 12% , SD = 0.5) during the fifth, and ($\bar{\chi}$ = 13% , SD = 0.6) during the final occasion.

Survival Modeling— The first set of models included 52 lactating females with measures of IFBFat. I found no evidence to suggest female body condition measured in autumn, determined by percent IFBFat, was associated with survival of neonates (ΔBIC was > 10 and 95% CI for the estimate overlapped 0); thus I continued on to the second stage of modeling that included 125 lactating females. Survival models that included time-dependent covariates (age of the neonate and time of season), and corresponding time-varying distance to escape terrain received nearly 100% of the model weight (Table 2). I selected the top ranked model containing neonate age, and average distance to escape terrain selected during early and late April.

The standardized ß-coefficients of the top model explaining survival of neonates indicated the odds of bi-weekly survival strongly increased as neonates aged (ß =1.02, SE=0.29) and slightly decreased with increasing distances from escape terrain (ß = -0.22, SE= 0.05) for individuals in April (Table 3). Probability of survival was lowest during the first-few weeks post-partum and early in the season when lactating females selected for habitat farther from escape terrain. When lactating females selected for habitat >100m from escape terrain, the probability of a neonate born in early April surviving to the next occasion was very low ($\bar{\chi}$ = 0.32, SE = 0.095), survival increased for those born in late April ($\bar{\chi}$ = 0.56, SE = 0.126), and continued to increase for neonates born in early May ($\bar{\chi}$ = 0.97, SE = 0.014), late May($\bar{\chi}$ = 0.99, SE = 0.002) and remained very high ($\bar{\chi}$ = 0.99, SE < 0.01) through the remainder of the season (Figure 3). Neonates born in early April had the lowest probability of surviving the 90 day neonatal period ($\bar{\chi}$= 0.17, SE= 0.09, n=15). Neonates born in late April had 3 times higher probability of surviving than those born in early April ($\bar{\chi}$= 0.54, SE= 0.05, n=26). Probability of survival continue to increase later in the season; probability of survival for neonates born in early

May was ($\bar{\chi}$= 0.983, SE= 0.03, n=39), increased slightly in late May ($\bar{\chi}$ = 0.99.4, SE= 0.04, n=32) and remained very high and stable ($\bar{\chi}$ < 0.99.8) for lambs born later in the season (n=13).

Neonates whose mothers remained closer to escape terrain had much higher chances of survival than those born to females that selected habitat farther (Figure 4). If a female selected for habitat that was on average 1m from escape terrain, the probability of a neonate born in early April to survive to the next occasion was ($\bar{\chi}$ =0.81, SE=0.04) but sharply dropped to ($\bar{\chi}$ = 0.31, SE=.095) at 100m, and ($\bar{\chi}$ = 0.05 , SE= 0.04) at 200m. My graphical estimations of goodness of fit showed that distance to escape terrain has a strong relationship, but that distances beyond 150m may have been high-leverage points, I did not remove those points, however, because they represented the variation in observed selection of habitat by lactating females.

DISCUSSION

When adult survival is high and stable, juvenile recruitment is the vital rate with the greatest potential to improve population trajectories (Gaillard et al. 2000, Raithel et al. 2007). Identifying factors that influence mortality risk for juveniles is complex because risk changes as juveniles age and many factors often interact and disguise the effect of one another. Juvenile mortality is often concentrated during the neonatal period, thus to develop effective management strategies for recovering endangered populations it’s important to determine the primary factors influencing mortality risk. I examined whether nutrition, predation, or quality of habitat selected by lactating females had the greatest effect on survival of Sierra bighorn sheep neonates. I also evaluated whether inbreeding depression was negatively influencing survival. I did not find evidence to suggest that inadequate nutrition or selection of poor quality habitat was a primary factor limiting survival of Sierra bighorn sheep neonates. Rather, I found that predation risk was the primary driver of survival, and that vulnerability of neonates to predators was highest for early-born neonates, neonates farther from escape terrain, and that vulnerability decreases as neonates aged. Understanding factors that increase risk of mortality for neonates can contribute to the development of strategies that can reduce mortality and potentially improve population dynamics.

I found no evidence to support the hypothesis that nutrition was a primary factor affecting survival of Sierra bighorn sheep neonates. I hypothesized that nutritional condition of females would strongly affect body condition of neonates and ability of females to care for neonates, yet none of the models containing female body condition (percent fall IFBFat) were competitive, and the estimated 95% CI overlapped 0. Although nutrition can limit the reproductive success for many species of ungulate, percent body fat of female Sierra bighorn was higher than is expected to inhibit pregnancy for elk (>5%, Cook et al. 2004*a*) and caribou (6 –7.8%; Crête et al. 1993, Ouellet et al. 1997), and does not suggest that lactating females within my sample were nutritionally stressed. I therefore rejected the hypothesis that poor body condition was negatively affecting survival of neonatal Sierra bighorn sheep.

I found no evidence to support the hypothesis that selection of poor quality habitat by lactating females during the neonatal period was a primary factor affecting survival of Sierra bighorn sheep neonates. None of the models containing habitat quality were competitively ranked and the 95% CI for coefficient estimates overlapped 0. Females within our sample selected habitat that, on average, was relatively high quality with little variation. Although the multidimensional estimate of habitat quality did not appear to relate to survival of neonates, when key resources within an RSF have very strong effects on selection of habitat, these isolated resources often yield an improved explanation of spatial survival patterns (DeCesare et al. 2012).

I found strong evidence to support the hypotheses that vulnerability of neonates to predators would be highest during the first few weeks of life and for neonates in habitat farther from escape terrain. I found mortality was concentrated within the first few weeks post-partum but probability of survival increased steadily increased and remained very high after one month old. As strength and mobility of neonates improve, they may be less vulnerable to predators. I also predicted that neonates born to females that selected habitat farther from escape terrain would have decreased survival because of the decreased likelihood of evading predators. I found probability of survival decreased with increasing distance from escape terrain, especially at distances beyond 150m. Neonatal lambs follow lactating females immediately from birth (Lent 1974), thus if pairs encounter a predator and flee to safety, neonates that have decreased mobility are much less likely to reach escape terrain than adults (Berger 1991, Bleich 1999). I found that beyond distances of approximately 200m from escape terrain neonates born in early April had less than 5% chance of survival. Although few females ventured beyond 200m, this suggests predators are highly successful at capturing neonates encountered at this distance. Escape terrain decreases risk of predation, however, those areas may provide less access to high quality forage (Festa-Bianchet 1988, Wehausen 1996, Rachlow and Bowyer 1998, Hamel and Côté 2007). Thus, I hypothesize that lactating females may have selected habitat farther from escape terrain to increase access to high quality forage. In a post-hoc analysis, I tested for a correlation between selection for distances to escape terrain and female IFBfat, but found no evidence to suggest that females who selected for distances farther from escape terrain did so because they were in compromised body condition and needed to obtain forage. It remains uncertain why lactating females would select for distances far from escape terrain where the probability of survival for neonates is so low.

Although predation by mountain lions has been a leading cause of mortality for adult Sierra bighorn sheep (Johnson et al. 2013, Stephenson et al. 2012) and bobcats have been known to take yearling bighorn sheep (T. Stephenson, California Department of Fish and Wildlife, unpublished data), I found no evidence to suggest that females who selected habitat where risk of encountering ambush predators was higher suffered higher rates of neonatal mortality. I found lactating females selected habitat where the average probability of encountering a lion was low (13%). Therefore, I hypothesize that predation-related mortalities of neonatal Sierra bighorn may primarily be attributed to coyotes or golden eagles. If I had included covariates for risk of predation by coyotes and golden eagles, I predict my results may have reflected increased mortality risk for neonates with increased encounter risk of coyotes and eagles. For neonatal Dall's sheep (*O. dalli*) in Alaska, 45% of mortalities were attributed to predation by coyotes, and 34% were golden eagles (Arthur and Prugh 2010). Golden eagle attacks were also most frequent during the first month post-partum for Dall's sheep in Alaska (Scotton 1998) and mountain goats (*Oreamnos americanus*) in Alberta, Canada (Hamel and Côté 2009).

I evaluated effects of predation and nutrition simultaneously by examining the influence of timing of birth on survival of neonates. I found neonates born the earliest (April) had the lowest chances of surviving and neonates born later during the season had the highest survival. Thus, I did not find support for the hypothesis that inadequate nutrition is affecting survival of neonates. I found no evidence to suggest neonates presumed to be in good body condition and having greater access to forage had higher survival than neonates expected to be in poor condition. My results support the hypothesis that predation is the primary cause of morality. Follower species with precocial young are expected to exhibit synchronized birth patterns as an antipredator strategy that satiates predators thus reducing the morality risk for neonates (Sinclair et al. 2000). Early-born neonates are much less likely to receive the benefits of group vigilance and defense because pregnant females generally remain on winter ranges until immediately prior to giving birth (Smith et al. 2014). I documented < 20 births before April 15th and no more than 2 births occurred in the same subpopulation in the same year, suggesting that lactating females who give birth before April 15th are likely to be isolated for several weeks post-partum. Although solitary lactating bighorn can successfully defend juveniles from predators, my results support the hypothesis that neonates born later are less vulnerable to predators (Berger 1978, Risenhoover and Bailey 1985, Mooring et al. 2004). Adams et al. (1995) found that early-born caribou calves had decreased survival as a result of increased predation risk, and hypothesized this could be attributed to an insufficient numbers of neonates to swamp predators or that early-born calves were the first to form nursery groups, thus they were highly detectable by predators. The sharp increase in probability of survival for neonatal lambs that coincides with the peak birthing period (May) further suggests neonates born during this time benefit the most from a synchronous lambing period (Estes 1976).

My results suggest that variation in vulnerability to predation risk and subsequent survival of neonates may explain the observed annual variation in juvenile recruitment. The relative influence of neonatal mortality on juvenile recruitment can be interpreted along a continuum of additive or compensatory effects on population growth (Monteith et al. 2014). When predators consume prey in poor nutritional condition that already had low probability of survival, the mortality is generally considered compensatory; however, when predators take prey that would otherwise have high probability of survival, mortality is considered additive (Errington 1956). A review by Linnell et al. (1995) found that mortality of neonates averaged 47% in populations with predators (n=68), but only 19% in populations without predators (n=6), suggesting mortality by predators may commonly have additive effects. Early-born neonates are expected to be born in good body condition and have extended access to high quality forage. In the absence of predators, I would expect high survival for early-born neonates, thus I hypothesize that predation on early-born neonates may have an additive effect on mortality of Sierra bighorn neonates.

I hypothesized that inbreeding depression would increase risk of mortality for neonates. I found no evidence that bi-weekly survival of neonates increased with increasing female heterozygosity. I expected that female heterozygosity indicates general quality and is associated with other factors that I was not able to directly measure, such as neonatal birth mass and immune system response (Sausman 1984, Slate et al. 2000, Hogg et al. 2006, Da Silva et al. 2009). Inbred neonatal Red deer (*Cervus elaphus*) in Scotland had much smaller birth weights than outbred calves, and increased rates of mortality (Coulson et al. 1998). It is possible that I did not detect a relationship between neonatal survival and female heterozygosity because there may not be a strong enough relationship between female heterozygosity and neonatal heterozygosity. Thus, it is possible that if inbred female bred a high heterozygosity ram, the resulting neonate could have higher heterozygosity than female heterozygosity alone would predict. Alternatively, it is possible that inbred lambs may suffer greater mortality risk after the neonatal period when maternal care is reduced. My results support the findings of Johnson et al. (2011) and suggests that although inbreeding depression can adversely affect fecundity, it is unlikely to influence survival of neonates.

I made several assumptions that if violated could affect my inferences. If the GPS locations included were imprecise my estimates of vulnerability to predators could be biased, to mitigate this, however, I only included GPS locations that had high estimates of geographic precision. Nest-survival models assume probability of detection is 100%, my estimated probability of detection was imperfect and it is possible that I did not observe a lamb that was present and considered it to have died. However, this is unlikely given the probability of missing a lamb was only 1%. Furthermore, I included several neonates with large time gaps between last observed alive and first observed dead, which can affect estimates of time to death. My model estimates, however, match externally estimated time to death for mortalities not included within the model (n= 68) where time of death was known.

MANAGEMENT IMPLICATIONS

Understanding the processes that influence population demographics can help managers better predict the effects of potential management alternatives. Examining the link between exposure to predation risk and probability of mortality for neonates allows managers to better understand the effects of predation risk on juvenile recruitment. My survival estimates for Sierra Nevada bighorn sheep suggest that survival of neonates can fluctuate widely depending on proximity to escape terrain selected by lactating females, if females remain closer to escape terrain my estimates suggest survival of neonates would increase. If females are selecting habitat farther from escape terrain to obtain higher quality forage, managers may be able to entice females to remain closer by improving nutritious forage near escape terrain by implementing prescribed burns (Greene et al. 2012).

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Table 1. Factors hypothesized to influence survival of neonatal Sierra Nevada bighorn sheep from 2006–2017 in Sierra Nevada, California, USA. H1-H4 = Primary hypothesized drivers of survival for neonates; H1.a) = hypothesized factors affecting vulnerability of neonates to primary hypothesized driver of survival.

Hypothesis	Predicted effect	Model covariate
H1: Habitat quality has the strongest effect on neonatal survival		
Habitat Quality	Females that select higher quality habitat will increase survival of neonates	Habitat quality, measured by resource selection (Chapter 1)
H2: Nutrition has the strongest effect on survival of neonates		
Factors that can affect nutrition of neonates		
H2.a) Female body condition	Increased body fat of lactating females will increase survival of neonates	Percent IFBFat of lactating female
H2.b) Timing of birth	Early-born neonates will have higher survival than late born	Timing of birth: (combinations of April and July-September)
H2.c) Female body condition + timing of birth	Low body fat of lactating females and late- birth will decrease survival of neonates AND High body fat and early-birth will increase survival of neonates	Percent IFBFat + Timing of birth (combination of April and July-September)
H3: Predation has the strongest effect on survival of neonates		
Factors that can affect vulnerability of neonates to predators		
H3.a) Age of neonate	Survival will increase with age	Age of neonate
H3.b) Selection of habitat (Encounter of ambush predators)	Selection of habitat where risk of encounter is high will decrease survival of neonates	Probability of encountering a mountain lion

H3.c) Selection of habitat (Escape terrain)	Selection of habitat far from escape terrain will decrease survival of neonates	Maximum distance to escape terrain
H3.d) Timing of birth relative to birth pulse	Survival will be low for early-born neonates	Timing of birth (early April, and early + late April)
H3.e) Combinations of age of neonate + timing of birth + combinations of selection of habitat	Survival will be increase with age, be low for early-born neonates, and decrease if lactating females use habitat with higher risk of predation	Age of neonate+ Timing of birth+ combinations of habitat selection

H4) Inbreeding depression will have negative effects on survival of neonates in combination with nutrition, predation, or habitat quality

Female body condition + Inbreeding depression	Increased body fat of lactating females will increase survival of neonates	Percent IFBFat of lactating female+ female heterozygosity
Timing of birth +Inbreeding depression	Early-born neonates will have higher survival than late born,	Timing of birth: (combinations of April and July-September) + female heterozygosity
Female body condition + timing of birth + Inbreeding depression	Low body fat of lactating females and late- birth will decrease survival of neonates AND High body fat and early-birth will increase survival of neonates	Percent IFBFat + Time of birth (combination of April and July-September) + female heterozygosity
Age of neonate strongly affects predation risk	Survival will increase with age	Age of neonate + female heterozygosity
Selection of habitat (encounter of ambush predators) + Inbreeding depression	Selection of habitat where risk of encounter is high will decrease survival of neonates	Probability of encountering a mountain lion (Chapter 1) + female heterozygosity

Selection of habitat (Escape terrain) + Inbreeding depression	Selection of habitat far from escape terrain will decrease survival of neonates	Maximum distance to escape terrain + female heterozygosity
Timing of birth relative to birth pulse+ Inbreeding depression	Survival will be low for early-born neonates	Timing of birth (early April, and early + late April) + female heterozygosity
Combinations of age of neonate + timing of birth + combinations of selection of habitat + Inbreeding depression	Survival will be increase with age, be low for early-born neonates, and decrease if lactating females use habitat with higher risk of predation	Age of neonate+ Timing of birth+ combinations of habitat selection + female heterozygosity

Table 2. Top ranked models for nest-survival analysis of neonatal Sierra Nevada bighorn sheep in the Sierra Nevada, California, USA from 2006–2017. Only models that were ranked higher than the constant model (.) are shown. K= number of parameters; BIC = Bayesian Information Criterion; ΔBIC = difference between BIC of model and the top model; ωi= model weight compared to all other models; Age= neonate age; Time # = Encounter occasion referring to seasonal time (eg. Time 1 refers to April 1st-15th); DE_mean= average distance from escape terrain for the specified time period; HET=percent heterozygosity of lactating females; Prisk_mean= average probability of encountering a hunting mountain lion during specified time period; HabQuality= average habitat quality selected by lactating females during the specified time period; PRisk_max= max probability of encountering a hunting mountain lion during specified time period; (.)= constant survival.

Model	*K*	BIC	ΔBIC	ω_i	Deviance
{Age + DE_mean+ Time1,2}	3	198.0	0.0	0.6	179.6
{Age + DE_mean *Time1,2}	4	200.6	2.6	0.1	175.0
{Age+DE_mean*Time1}	4	200.9	2.9	0.1	175.9
{Age+ DE_max+Time1,2}	3	202.3	4.3	0.1	184.0
{Age + DE_mean1,2,3}	3	202.7	4.8	0.0	184.4
{Age+ DE_mean1,2*Time1,2}	5	205.1	7.1	0.0	174.5
{Age + Time1,2}	3	209.7	11.7	0.0	191.3
{Age*DE_mean1,2* Time1,2}	6	210.8	12.8	0.0	174.1
{DE_mean*Time1,2}	3	214.8	16.8	0.0	196.4
{Age}	2	215.1	17.1	0.0	202.9
{Age*Time1,2,3}	5	217.5	19.5	0.0	187.0
{Age*Time1,2 +HET}	5	218.3	20.3	0.0	187.7
{Age*Time1,2, PRisk_mean1,2}	5	219.1	21.1	0.0	188.6

{Age*Time1,2, HabQuality1,2}	5	219.8	21.8	0.0	189.3
{Age*Time1,2, PRisk_max+Time1,2}	5	220.0	22.0	0.0	189.4
{Time1,2,3}	4	221.1	23.2	0.0	196.7
{Age*Time1,2 +DE_max+Time1,2}	6	221.3	23.4	0.0	184.7
{Age*Time1,2,3,4}	6	223.5	25.5	0.0	186.8
{Time_1,2}	3	224.6	26.7	0.0	206.3
{ALL_time1:6}	6	225.5	27.6	0.0	188.9
{.}	1	255.4	57.4	0.0	249.2

Table 3. Standardized parameter estimates from the top nest survival model explaining survival of neonatal Sierra Nevada bighorn sheep in the Sierra Nevada of California, USA from 2006–2017. Intercept= includes May- September 30th; Lamb Age= age of neonate (14 day increments); Distance to Escape Terrain (distance in meters from slopes >42°).

Covariate	β	SE	LCI	UCI
Intercept	0.429	0.507	-0.566	1.423
Lamb Age	1.018	0.294	0.441	1.595
Distance to Escape Terrain	-0.022	0.005	-0.032	-0.012

Figure 1. Study area in southeastern Sierra Nevada of California. Herds extend from Mt. Warren near Lee Vining, CA south approximately 200km to Olancha, CA. Study subpopulations are outlined in orange and include: Mt. Warren, Mt. Gibbs (Northern Recovery Unit); Convict Creek, Wheeler Ridge (Central Recovery Unit); Mt. Baxter, Sawmill Canyon and Mt. Langley (Southern Recovery Unit).

Figure 2. Parturition dates for neonatal Sierra Nevada bighorn sheep (n=125) between 2006-2017 in the Sierra Nevada of California, USA binned into bi-weekly intervals.

Figure 3. Predicted bi-weekly survival of neonatal Sierra Nevada bighorn sheep between 2006–2017 in the Sierra Nevada of California, USA illustrated for a mean selected distance from escape terrain of 100m when a lamb is 14 days old. Solid line represents bi-weekly survival rate estimated using beta parameters from the top model, vertical lines represent upper and lower 95% confidence intervals for the estimated bi-weekly survival rate.

Figure 4. Predicted bi-weekly survival of neonatal Sierra Nevada bighorn sheep in relation to average distance to escape terrain selected by lactating females with lambs during April between 2006–2017 in the Sierra Nevada of California, USA. Illustrated for the first two encounter occasions (color coded). Center solid lines represent mean bi-weekly survival estimate, shaded regions represents 95% confidence intervals. Observed survival outcomes are denoted as triangles for neonates that survived to recruitment and circles for neonates that died before recruitment and indicate the average distance selected by lactating females during both encounter occasions in April

.

Figure 1.

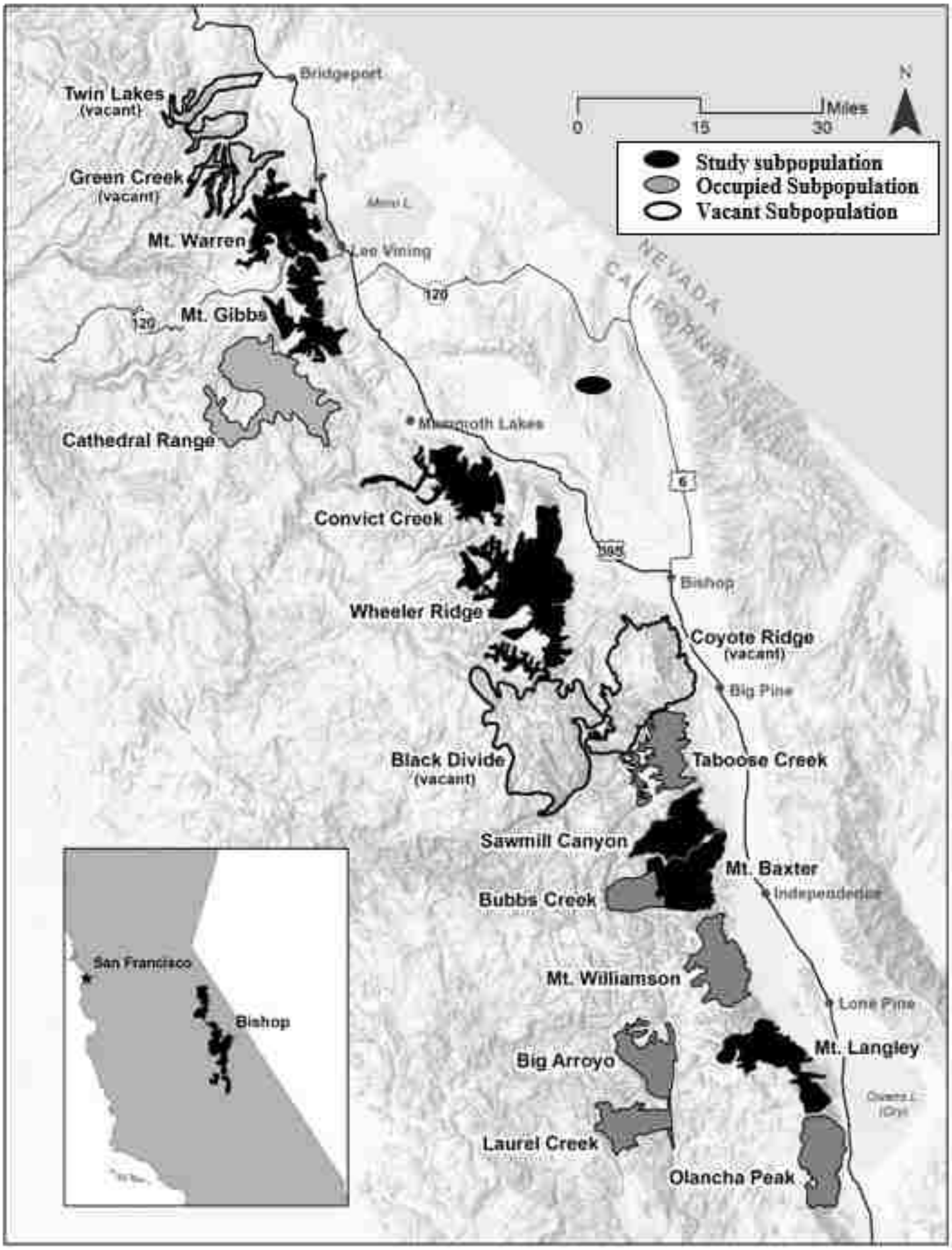

Bridgeport
Twin Lakes (vacant)
Green Creek (vacant)
Mono L.
Mt. Warren
Lee Vining
120
Mt. Gibbs
120
Cathedral Range
Mammoth Lakes
NEVADA
CALIFORNIA
6
Convict Creek
395
Bishop
Wheeler Ridge
Coyote Ridge (vacant)
Big Pine
Black Divide (vacant)
Taboose Creek
Sawmill Canyon
Mt. Baxter
Bubbs Creek
Independence
Mt. Williamson
Lone Pine
Mt. Langley
Big Arroyo
Owens L. (Dry)
Laurel Creek
Olancha Peak
N
0
15
30
Miles
Study subpopulation
Occupied Subpopulation
Vacant Subpopulation
San Francisco
Bishop

Figure 2.

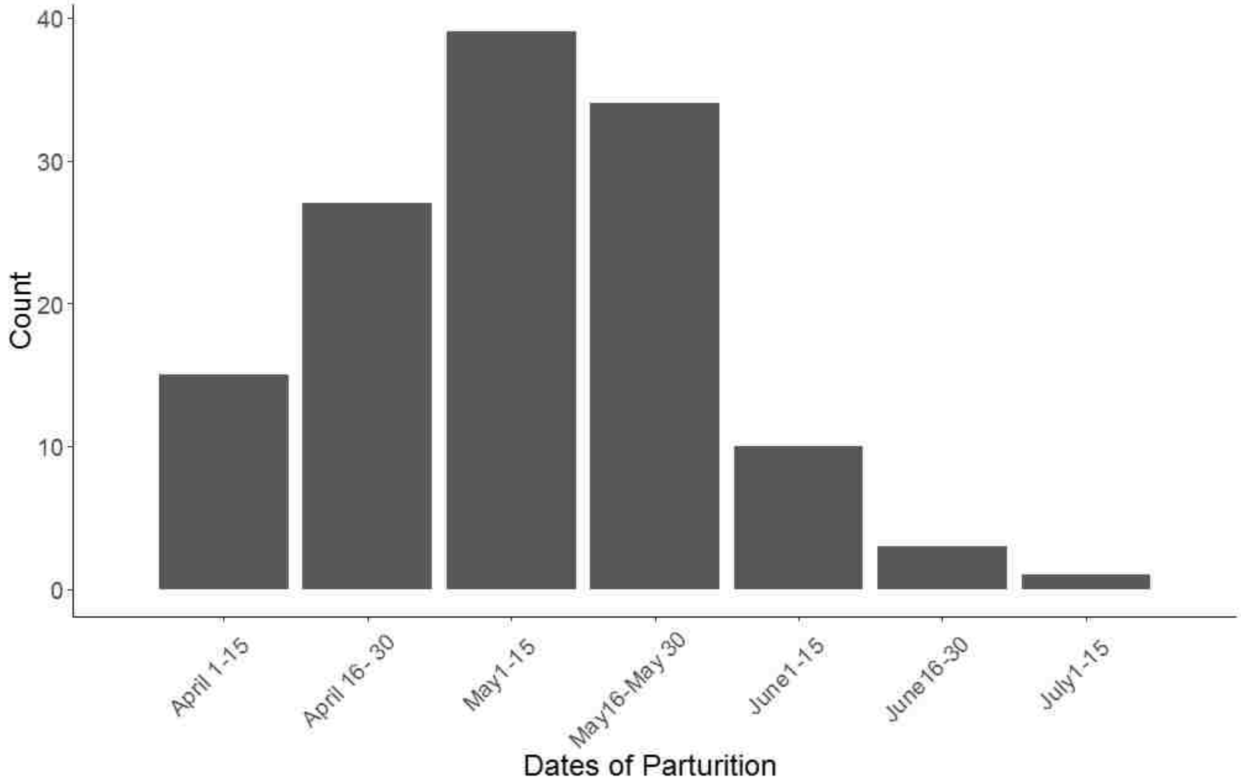
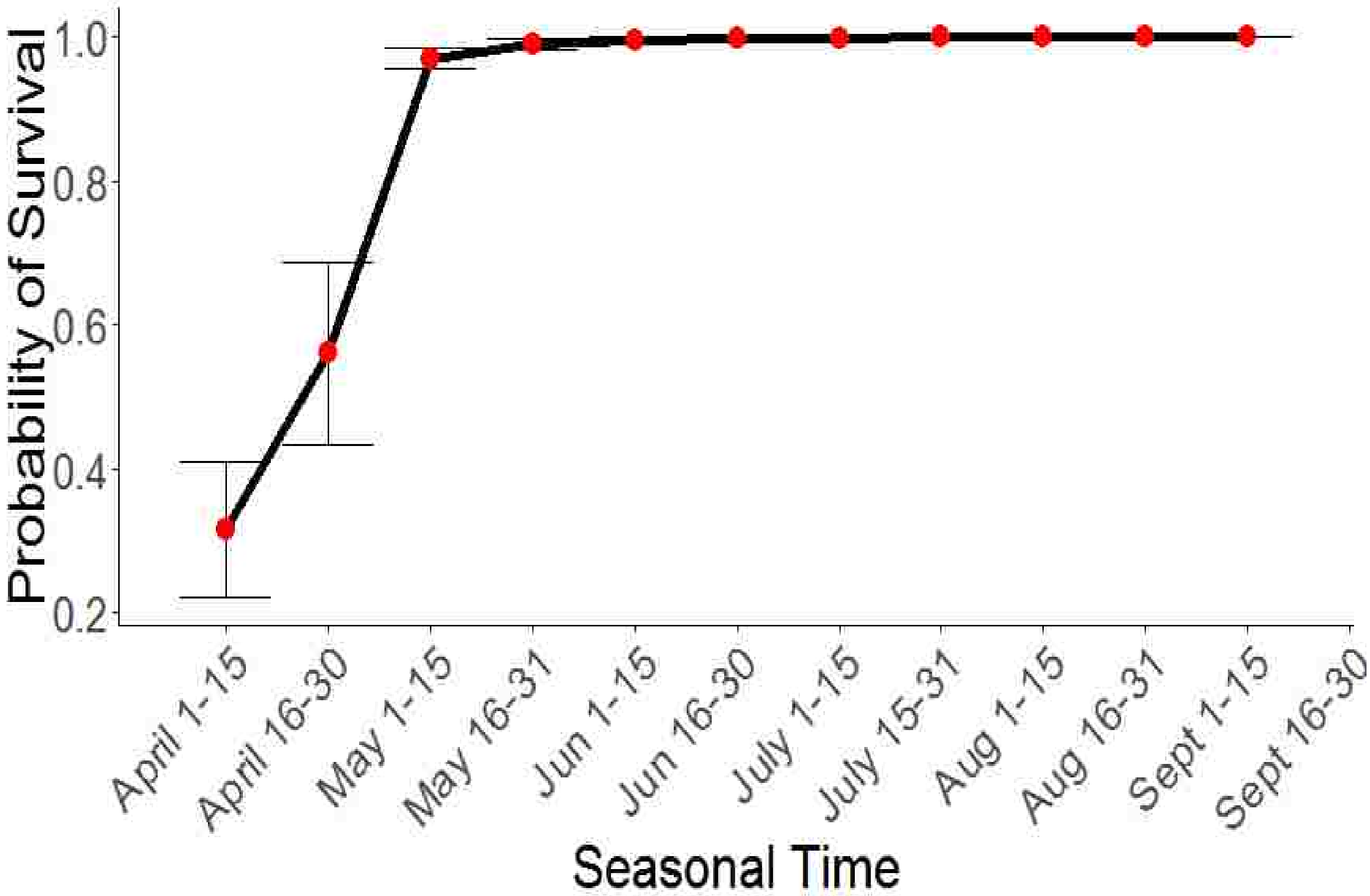
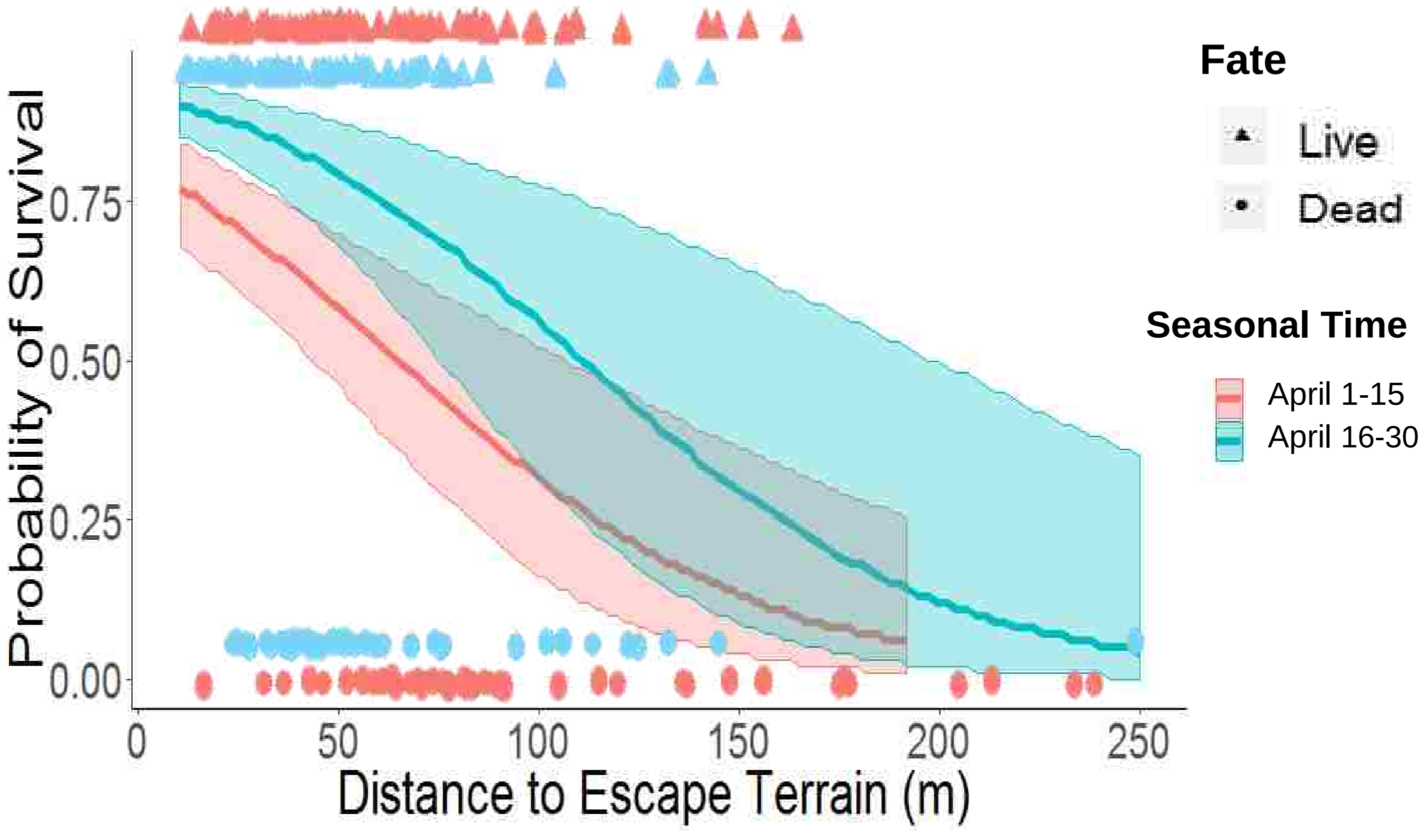

40
30
20
10
0
Count
April 1-15
April 16 - 30
May1-15
May16-May 30
June1-15
June16-30
July1-15
Dates of Parturition

Figure 3.



Probability of Survival
1.0
0.8
0.6
0.4
0.2
April 1-15
April 16-30
May 1-15
May 16-31
Jun 1-15
Jun 16-30
July 1-15
July 15-31
Aug 1-15
Aug 16-31
Sept 1-15
Sept 16-30
Seasonal Time

Figure 4.



Fate
▲ Live
● Dead
Seasonal Time
April 1-15
April 16-30
Probability of Survival
0.00
0.25
0.50
0.75
0
50
100
150
200
250
Distance to Escape Terrain (m)