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CONSERVATION ECOLOGY - ORIGINAL RESEARCH

Evaluating apparent competition in limiting the recovery of an endangered ungulate

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Abstract Predation can disproportionately affect endangered prey populations when generalist predators are numerically linked to more abundant primary prey. Apparent competition, the term for this phenomenon, has been increasingly implicated in the declines of endangered prey populations. We examined the potential for apparent competition to limit the recovery of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), an endangered subspecies under the US Endangered Species Act. Using a combination of location, demographic, and habitat data, we assessed whether cougar (*Puma concolor*) predation on endangered bighorn sheep was a consequence of their winter range overlap with abundant mule deer (*Odocoileus hemionus*). Consistent with the apparent competition hypothesis, bighorn sheep populations with higher spatial overlap with deer exhibited higher rates of cougar predation which had additive effects on adult survival. Bighorn sheep killed by cougars were primarily located within deer winter ranges, even though those areas constituted only a portion of the bighorn sheep winter ranges. We suspect that variation in sympatry between bighorn sheep and deer populations was largely driven by differences in habitat selection among bighorn sheep herds. Indeed, bighorn sheep herds that experienced the highest rates of predation and the greatest spatial overlap with deer also exhibited the strongest selection for low elevation habitat. Although predator-mediated apparent competition may limit some populations of bighorn sheep, it is not the primary factor limiting all populations, suggesting that the dynamics of different herds are highly idiosyncratic. Management plans for endangered species should consider the spatial distributions of key competitors and predators to reduce the potential for apparent competition to hijack conservation success.

Keywords Conservation · Cougar · *Ovis canadensis sierrae* · Predation · Sierra Nevada bighorn sheep

Introduction

Predation can disproportionately affect endangered prey populations when generalist predators are numerically linked to more abundant primary prey (Sinclair et al. 1998; McLellan et al. 2010; DeCesare et al. 2010). Depending on the rate of predation, whether mortalities are additive or compensatory, and which stage classes are killed (Mills 2007), the opportunistic take of secondary prey can yield dramatic population declines (Roemer et al. 2002; Bryant and Page 2005). This phenomenon has been termed "apparent competition" (Holt 1977; Holt and Lawton 1993), as the asymmetrical influence of a shared predator on the abundance of primary and secondary prey can

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appear as if the species were in direct competition with one another. While prey population declines may initially occur due to factors such as habitat loss, overexploitation, or disease, once populations become small they are highly vulnerable to predators subsidized by other prey. Depending on the functional response of predators to endangered prey (Holling 1959), apparent competition can lead to either the extirpation of a secondary prey population or trap them in a "predator pit" where low numbers of prey remain but the population is inhibited from recovery (Messier 1994; Sinclair et al. 1998).

Apparent competition has been implicated in limiting the recovery of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*; hereafter bighorn sheep; Gibson 2006; DeCesare et al. 2010), the rarest subspecies of mountain sheep in North America, and listed as endangered by the US Endangered Species Act (US Fish and Wildlife Service 2007). Population declines initially occurred in the 1800s due to disease, unregulated market hunting, and competition with livestock. More recently, however, population declines have been attributed to predation by cougars (*Puma concolor*; Wehausen 1996; US Fish and Wildlife Service 2007). While there are estimated to be <400 bighorn sheep in the Sierra Nevada (http://www.dfg.ca.gov/snbs/Literature.html) thousands of mule deer (*Odocoileus hemionus*) winter in close proximity to endangered herds and serve as the primary prey source for cougars (Pierce et al. 1999, 2000). Bighorn sheep and deer do not strongly compete for forage [California Department of Fish and Game (CDFG) unpublished data], but their spatial proximity to one another may exacerbate cougar predation on endangered bighorn herds, potentially limiting recovery success.

The bighorn–deer–cougar ecosystem in the eastern Sierra Nevada exhibits several characteristics classically associated with predator-mediated apparent competition (Holt 1977; Holt and Lawton 1994; Chaneton and Bonsall 2000; DeCesare et al. 2010). For example, cougars are generalist predators with high mobility between the ranges of both prey species. The deer population (~19,000) is dramatically larger than the bighorn sheep population (~360), and has a higher potential for population growth due to twinning. Additionally, about 75 % of mortalities of collared bighorn sheep have occurred during winter months (December–April) when the ranges of bighorn sheep and deer (and, thus, cougars) have the greatest potential for overlap. While some herds of bighorn sheep consistently inhabit areas adjacent to the winter ranges of deer and cougars, other herds appear to exist in areas of low deer and cougar density. This variation has created uncertainty about the demographic impact of cougar predation on this subspecies and the utility of predator management as a recovery strategy. Given that cougars are an abundant, yet protected, species in California (Torres et al. 1996), clarifying the causes and consequences of cougar predation on bighorn sheep is critical for directing appropriate management actions for endangered bighorn sheep recovery.

Our objective was to examine spatial predictions of the apparent competition hypothesis for Sierra Nevada bighorn sheep, testing whether cougar predation on bighorn sheep populations may be a function of the degree of sympatry between bighorn sheep and deer. If apparent competition was responsible for cougar predation on bighorn sheep, we predicted that bighorn populations with greater spatial overlap with deer would have higher rates of predation, and that predation would have associated demographic consequences (Holt 1977; Holt and Lawton 1994). We also predicted that cougar predation on bighorn sheep would most likely occur in locations known to be sympatric between bighorn sheep and deer (James et al. 2004), rather than in locations exclusively used by bighorn sheep. Additionally, because Johnson et al. (2010b) observed considerable discrepancies in habitat characteristics among bighorn sheep populations, we evaluated whether variation in habitat selection across herds contributed to differences in their spatial overlap with deer. We evaluated these predictions in four populations of bighorn sheep that span the geographic range of the subspecies, encompass a majority of the bighorn sheep in the Sierra Nevada, and have exhibited widely varying population dynamics (Johnson et al. 2010a, b).

Materials and methods

Study area and populations

We examined bighorn sheep populations that have been the focus of extensive data collection in the Sierra Nevada mountains, California. Situated north to south along the Sierra Nevada escarpment these populations are Mono Basin, Wheeler Ridge (Wheeler), Mt Baxter and Sawmill Canyon (Baxter), and Mt Langley (Langley; Fig. 1), representing approximately 85 % of all bighorn sheep in the subspecies. Bighorn sheep spend summers in the alpine and winters either in the alpine or at lower elevations typically east of the crest, inhabiting an elevation range from 1,525 to >4,000 m (US Fish and Wildlife Service 2007; see Johnson et al. 2010a for additional information on study populations and study areas). Deer in the vicinity spend winters on the east side of the Sierra Nevada Crest, typically at elevations between 1,200 and 2,400 m. Cougars are closely tied to local deer herds, migrating with them seasonally as deer comprise their primary food source (Pierce et al. 1999, 2000).

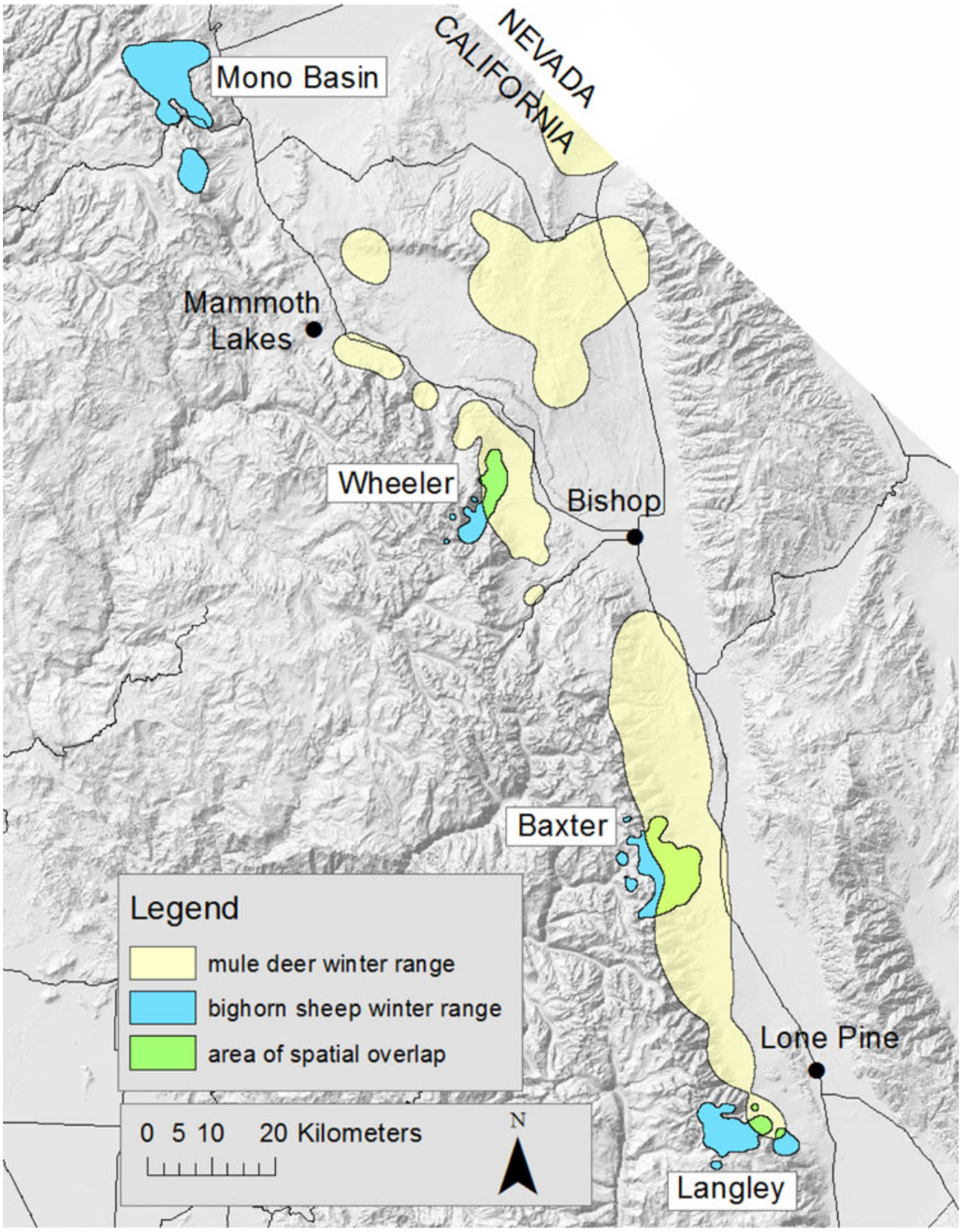

Fig. 1 Winter ranges of the Mono Basin, Wheeler, Baxter, and Langley populations of Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*), with their respective areas of overlap with mule deer (*Odocoileus hemionus*) based on the 90 % probability density distributions from locations of each species, California, USA

Quantifying spatial overlap in winter ranges of bighorn sheep and deer

To quantify the degree of spatial overlap between the winter ranges of bighorn sheep and mule deer, we used locations collected December–April during the winters of 2002–2010. We obtained bighorn sheep locations from a combination of ground observations and global positioning system (GPS) collars. To obtain ground observations of bighorn sheep, experienced observers would survey winter ranges with binoculars and spotting scopes, recording the composition and location of each group. To obtain GPS collar locations, male and female bighorn sheep were captured and collared via helicopter net-gun operations (University of Montana Institutional Animal Care and Use Protocol 024-07MHWB-071807). GPS collars were initially deployed at Wheeler in 2002, at Baxter and Mono Basin in 2003, and at Langley in 2004; captures occurred 1–2 times/year through April 2010. We randomly selected one location/week from each GPS collared individual during the months of interest. Collars were manufactured by the companies Advanced Telemetry Systems (ATS), North Star Science and Technology (North Star), Lotek Wireless, and Televilt International.

To delineate the winter ranges of mule deer, we compiled locations from four distinct deer herds that potentially overlapped with bighorn sheep. Three of those herds, Casa Diable, Goodale, and Mono-Walker, were surveyed by helicopter in January and March 2002–2010 and the composition and location of each deer group was recorded. In the Round Valley herd, deer were captured with a helicopter net-gun (Idaho State University Institutional Animal Care and Use Protocol 650-0410) and GPS collars (ATS and Televilt International) were deployed on a subset of 80 females from the fall of 2002 through spring of 2009. We randomly selected 1 location/week from each collared deer from December to April to delineate winter range use.

We estimated spatial overlap between bighorn sheep and mule deer by creating contour polygons around the 90 % probability density distribution of locations for each population of each species. To model these distributions, we first calculated 80 % of the reference bandwidth (*h*) that was estimated for each dataset (Worton 1995; Kie et al. 2002) using Animal Space Use (Horne and Garton 2007). We then used a kernel density estimator (KDE; Worton 1989) with the respective *h* values in Hawthstools 3.27 (Beyer 2004) to calculate the spatial probability density function for each population of each prey species. From those functions, we generated 90 % volume contours (containing approximately 90 % of the locations used to create the kernel density estimate) and considered these to be the winter ranges. For each bighorn sheep population, we calculated the area (km^2) and proportion of winter range that overlapped with deer.

Testing spatial predictions of apparent competition

To assess the influence of predation on bighorn sheep, we used known-fate survival data from individuals marked with very high frequency (VHF) or GPS collars. Since 1999, bighorn sheep have been captured and collared 1–2 times/year in the Sierra Nevada. Collared individuals were monitored ≥twice monthly by ground and aerial telemetry to determine survival and cause-specific mortality. After a collar emitted a mortality signal, ground crews investigated the site to determine the cause of death based on evidence of predation, accidents, and nutritional condition; if the cause of death could not be ascertained the mortality was categorized as "unknown."

To evaluate our first spatial prediction of the apparent competition hypothesis, that greater habitat overlap with deer would result in higher cougar predation on bighorn sheep, we calculated cause-specific mortality rates for each population using nonparametric cumulative incidence functions (Heisey and Patterson 2006). Animals entered the study following a staggered entry design (based on initial capture date) and exited when they died or were censored due to collar failure ($n = 6$) or the end of the study (14 April 2010). We calculated mean annual mortality rates based on a biological year from 15 April to the following 14 April (the start of the lambing season). We calculated annual mortality rates for a population once the number of collared animals was ≥6 (numbers of collared animals/year/population ranged from 6 to 25). This resulted in annual data for Wheeler starting in 2002, for Mono Basin starting in 2003, for Baxter starting in 2005, and for Langley starting in 2006. Mortality causes were classified as cougar predation, physical injury (namely from falls or rock-slides), other (old age, road-kill, or malnutrition), and unknown.

We examined the demographic consequences of cougar predation by testing whether predation had additive effects on adult bighorn sheep survival, the vital rate with the highest elasticity for bighorn sheep relative to population growth (Gaillard et al. 2000; Johnson et al. 2010a). To do this, for each population we regressed annual cougar mortality rates against annual survival rates (Williams et al. 2002). If cougar predation additively influenced bighorn sheep survival, there should be an inverse relationship between predation and survival ($\beta = -1$), whereas if predation was compensatory, there should be no relationship between predation and survival ($\beta = 0$). To conduct this test, annual population-specific cougar predation rates were estimated using the method outlined above, while annual population-specific survival rates were estimated from Kaplan–Meier models (Pollock et al. 1989) using the same parameters as the cause-specific mortality analyses (i.e., biological year and time-frame of analysis/population). While this test has been broadly applied (Williams et al. 2002; Murray et al. 2010; Griffin et al. 2011), it has been found to be biased toward detecting additivity (Schaub and Lebreton 2004). To account for this bias, we calculated a corrected slope parameter (model slope divided by intercept; Burnham et al. 1984) and a corrected standard error of the slope using the delta method.

To evaluate our next prediction, that cougar predation on bighorn sheep would occur within habitat that overlapped with deer, we determined whether each cougar-killed sheep was located within the 90 % KDE of deer winter range. Kills of both collared and uncollared bighorn sheep were included in the analysis; uncollared sheep were found opportunistically during field activities associated with this project. If cougar kills occurred randomly throughout bighorn sheep winter ranges, we expected the proportion of kills within the 90 % KDE of deer to be equal to that proportion of overlap between the winter ranges of bighorn sheep and deer for each bighorn herd. We tested this expected value of kills against the observed number of kills within deer winter ranges using binomial probability tests.

Testing for differences in habitat selection among bighorn sheep populations

We employed mixed-effects resource selection models (RSFs) to examine whether differences in habitat selection among bighorn sheep populations contributed to observed patterns of sympatry between bighorn sheep and deer. For example, if herds of bighorn sheep exhibited differential selection for habitat characteristics like elevation or terrain ruggedness, we expected that they may exacerbate or reduce their spatial overlap with deer. We focused on bighorn sheep habitat selection during winter months (December–April), as this is the period when most cougar mortalities have occurred and when there is the greatest potential for habitat overlap between prey species. RSF models were generated from adult female GPS collar data collected during the winters of 2008 and 2009, following a use-availability design (Manly et al. 2002). For most collared females, we only obtained location data during one winter; for those females from which we had data from both winters, we analyzed selection separately each year.

Attributes associated with each GPS location were compared to three randomly selected locations within available habitat. For each population, available habitat was delineated by combining the 100 % winter minimum convex polygons (MCPs) of each collared female/year, representing 3rd order selection within an animal's home range (Johnson 1980). Because the ratio of used/unused locations is unknown in a use-availability design, we employed the exponential approximation to the logistic model (Johnson et al. 2006). This compares used and available locations to estimate a relative probability of use (w(x)):

$$w(x) = \exp\left(\beta_1 x_1 + \beta_2 x_2 + \cdots + \beta_\mathrm{p} x_\mathrm{p} + \gamma_{0\mathrm{j}}\right)$$

as a function of habitat covariates (x_i), their respective selection coefficients (β_i), and a random intercept for each animal- and year-specific dataset ($\gamma_{0\mathrm{j}}$). We included the random intercept to account for autocorrelation within datasets and differences in sample size among datasets (Gillies et al. 2006). A coefficient >0 indicated selection for a habitat covariate, whereas a coefficient of <0 indicated avoidance, with values estimated from covariate availability.

We included habitat covariates found most important in bighorn sheep habitat studies (Smith et al. 1991; Bleich et al. 1997, 2008; DeCesare and Pletscher 2006), focusing on factors related to topography and vegetation. Topographic variables included elevation, slope, aspect, and terrain ruggedness, derived from 30-m USGS Digital Elevation Models (DEMs). Elevation and slope values were determined directly from DEMs. Aspect was coded as a continuous variable from −1 to 1 following Cushman and Wallin (2002). We estimated terrain ruggedness using an index developed by Sappington et al. (2007), which incorporates heterogeneity in slope and aspect. To account for vegetation, we included a categorical variable for forested land cover types, as they are strongly avoided by bighorn sheep (Smith et al. 1991; DeCesare and Pletscher 2006). We used the dominant vegetation class in US Forest Service Calveg maps (http://www.fs.fed.us/r5/rsl/projects/mapping) to categorize pixels as either forested or nonforested (the reference class).

In addition to topographic and vegetation variables, we also evaluated bighorn sheep habitat selection with respect to risk of cougar predation. Wehausen (1996) concluded that bighorn sheep in the Sierra Nevada actively avoided winter ranges inhabited by cougars, and instead selected habitat at higher elevations. Given the implications of this behavior for mitigating cougar predation, we explicitly tested for this effect. We defined risk of predation as the relative probability of encountering a hunting cougar (Lima and Dill 1990; Hebblewhite and Merrill 2007). To estimate risk of predation, we used locations from cougars captured and collared in and around bighorn sheep habitat between 2002 and 2009. Each cougar was fitted with a GPS collar (North Star, Lotek Wireless or Televilt International) programmed to collect locations every 4, 6, or 8 h on revolving schedules. We used only winter data (December–April) and defined hunting locations as those collected between 1 h pre-sunset to 1 h post-sunrise (Pierce et al. 1998). We excluded "clusters" of locations indicative of feeding sites (Knopff et al. 2009), retaining only the first location from such feeding-site clusters to represent hunting. From those locations, we estimated a KDE (Hebblewhite and Merrill 2007) calculating h using likelihood cross-validation (Horne and Garton 2006) to obtain finer-scale density estimates. We validated our cougar predation risk layer with 48 out-of-sample cougar-killed bighorn sheep (e.g., Hebblewhite and Merrill 2007). We used Spearman's rank correlation to compare the area-adjusted frequency of predation risk values in bighorn sheep winter range to the number of cougar-killed sheep within the same frequency bins (Boyce et al. 2002). Based on sample size, we used 5 frequency bins. Our index of risk and kill sites had a coefficient of determination of 0.90 ($p = 0.04$), indicating that our layer strongly reflected risk of cougar predation for bighorn sheep.

We examined habitat covariates to determine that no two variables were highly related using correlation coefficients ($r > |0.6|$) and variance inflation factors (VIF > 5; Menard 1995). Elevation and predation risk were confounded and negatively correlated with one another (r for different populations ranged from 0.52 to 0.65), as predation risk increased in low elevation areas (Fig. 2). We removed elevation from multivariate analyses, and evaluated selection for elevation in a separate univariate analysis for each population. We conducted univariate tests of all habitat variables (Hosmer and Lemeshow 2000), using a cut-off value of $p = 0.1$ (based on Wald z statistics) for entry into habitat models. We also modeled all effects as

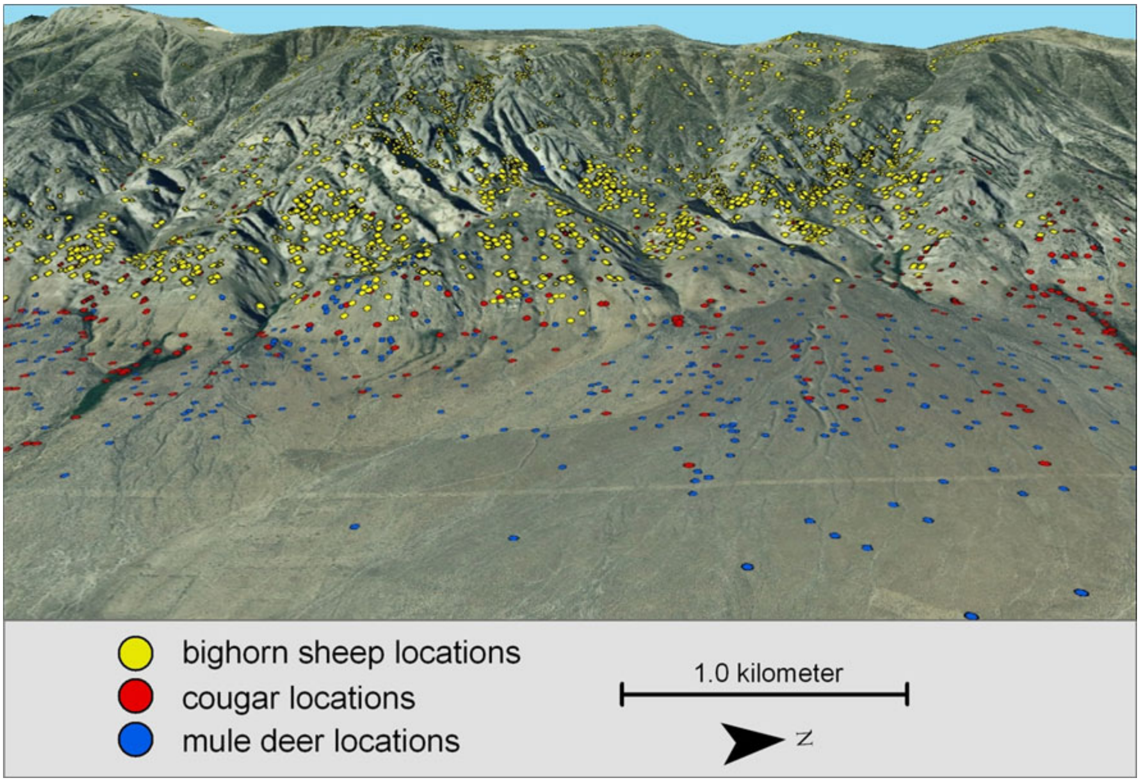

Fig. 2 Collar locations from bighorn sheep, mule deer, and cougars (*Puma concolor*) during winter along Wheeler Crest, California, USA. While locations demonstrate general differences in elevations used by each prey species, they also illustrate the overlap in habitat-use among prey species

linear because univariate tests revealed no nonlinear functions.

We ran the multivariate model for each bighorn sheep population, evaluating the direction and magnitude of selection for each habitat factor. Because a high number of collared bighorn sheep at Baxter afforded additional degrees of freedom to fit a more complex model, we tested whether selection for areas of high predation risk varied over the course of the winter by including a risk-by-date interaction for this population. Green-up commences at lower elevations in mid-winter in the study area, at elevations frequently used by deer and cougars (Greene 2010). As a result, we expected that there may be temporal variation in the relationship between habitat selection and risk as winter progressed.

We validated the predictive power of each herd-specific model with cross-validation (Boyce et al. 2002) using out-of-sample GPS locations collected during the winters of 2002 through 2006. We randomly selected 1,000 GPS locations from Wheeler, Baxter, and Langley, and 700 locations from Mono Basin (as there were fewer available locations), which were obtained from 13, 4, 6, and 3 adult females, respectively. Given the large sample size, we used 10 bins for cross-validation. All statistical analyses were conducted in STATA (StataCorp, College Station, TX, USA).

Results

Spatial overlap of winter ranges of bighorn sheep and deer

To delineate the winter ranges of bighorn sheep populations, we used 1,431 independent ground observations and 2,839 GPS locations from 102 bighorn sheep; 27, 39, 21, and 15 bighorn sheep in Mono Basin, Wheeler, Baxter, and Langley, respectively. In total, this provided 932 locations from Mono Basin, 2023 from Wheeler, 816 from Baxter, and 499 from Langley. To delineate deer winter range, we used 496, 1,169, and 1,173 helicopter locations from the Casa Diablo, Goodale, and Mono-Walker deer herds, respectively, and 1,181 locations collected from GPS collars from the Round Valley herd. The *h* values used to generate kernel density polygons from bighorn sheep locations were 1,383, 719, 856, and 886 for Mono Basin, Wheeler, Baxter, and Langley, respectively. From deer locations, the *h* values were 3,194, 3,587, 5,577, and 1,927 for the Casa Diablo, Goodale, Mono-Walker, and Round Valley herds, respectively. Given the 90 % kernel volume contours, the amount of spatial overlap between bighorn sheep and deer winter ranges varied considerably by population. There was no winter range overlap with deer in Mono Basin, 10.9 km^2 (14 % of the winter range) overlap with deer at Langley, 28.5 km^2 (58 %) overlap with deer at Wheeler, and 71.4 km^2 (67 %) overlap with deer at Baxter (Fig. 1; Table 1).

Spatial predictions of apparent competition

To quantify the direct effects of predators, we used survival data from 162 collared bighorn sheep; 39 bighorn sheep in Mono Basin, 53 in Wheeler, 44 in Baxter, and 26 in Langley. Of those, 62 died during the study: 17 in Mono Basin, 19 in Wheeler, 19 in Baxter, and 7 in Langley. Across all populations, 22 deaths were assigned to cougar predation, 9 to other factors, 8 to physical injury, and 23 were categorized as unknown.

Average annual cause-specific mortality rates for cougar predation were 0 in Mono Basin (no cougar predation detected), 0.03 in Langley, 0.05 in Wheeler, and 0.12 in Baxter (Table 1). As predicted from the apparent competition hypothesis, rates of cougar predation were positively correlated with the area of spatial overlap between bighorn sheep and deer ($r^2 = 0.99$, $p = 0.005$, $n = 4$). In Baxter and Wheeler, cougar predation was the primary mortality factor, while unknown factors were responsible for most mortality in Mono Basin and Langley (Table 1).

When annual survival rates from each population were regressed against their respective annual rates of cougar predation, the corrected regression slopes indicated that predation additively affected bighorn sheep survival (Fig. 3). The relationship between annual survival and cougar predation was highly correlated and statistically significant in Baxter and Wheeler, demonstrating a strong influence of cougar predation on annual survival rates in these herds. The relationship was weakly correlated and not statistically significant in Langley (Fig. 3).

A total of 48 (20 collared, 28 uncollared) cougar-killed bighorn sheep were located over the course of the study; 92 % were killed in locations sympatric between bighorn sheep and deer winter ranges. In Wheeler, 24 of 27 (89 %) cougar-killed bighorn sheep occurred within delineated deer winter range, but only 58 % of bighorn sheep range overlapped with deer (binomial probably test, $p < 0.001$). In Baxter, 17 of 18 kills (94 %) occurred within deer range and 67 % of bighorn sheep winter range overlapped with deer ($p = 0.007$). In Langley, there were only three cougar-killed sheep, but all of them occurred within delineated deer winter range; only 14 % of the bighorn sheep range overlapped with deer in that herd ($p = 0.003$).

Differences in habitat selection among bighorn sheep populations

To evaluate habitat selection, we deployed 32 GPS collars on adult female bighorn sheep; 5 in Mono Basin, 6 in Wheeler, 13 in Baxter, and 8 in Langley representing approximately 45, 17, 34, and 24 % of the total adult females in each herd, respectively. We collected GPS data for 1 year from 21 females (winter 2008 or winter 2009) and for both years from 11 females, providing a total of 7 animal- and year-specific datasets from Mono Basin, 10 from Wheeler, 17 from Baxter, and 10 from Langley to characterize winter habitat selection. In total, collars collected 21,350 locations with a GPS fix rate of 87 %. To estimate the cougar predation risk KDE, we used 5,673 GPS locations from 21 collared cougars; h was estimated to be 519.

From the multivariate models, we found that bighorn sheep in all populations avoided forested areas and selected for steeper slopes, rugged terrain, SSW aspects, and areas where they may encounter a cougar (except for Mono Basin which had no risk of predation), but different populations varied in their magnitude of selection for these attributes (Table 2; Fig. 4). Bighorn sheep on the winter ranges of Baxter and Wheeler experienced the greatest risk of cougar predation, and of those two herds, Baxter exhibited the strongest selection for risky habitat (Fig. 4). When we tested for a risk × date interaction with Baxter data, the population with the highest number of collared females (and the degrees of freedom to support the more

Table 1 Mean annual probabilities of cause-specific mortality, known-fate survival, and overlap with mule deer (*Odocoileus hemionus*) winter ranges for Sierra Nevada bighorn sheep (*Ovis canadensis sierrae*) populations, California, USA (±SE)

Population	Cause-specific mortality				Area	% Winter range
	Cougar	Injury	Other	Unknown	Deer overlap (km^2)	Deer overlap
Mono Basin	0.00 (0.00)	0.01 (0.01)	0.06 (0.02)	0.11 (0.03)	0	0
Wheeler	0.05 (0.02)	0.01 (0.01)	0.01 (0.01)	0.04 (0.01)	29	58
Baxter	0.12 (0.04)	0.04 (0.02)	0.02 (0.01)	0.03 (0.02)	71	67
Langley	0.03 (0.02)	0.02 (0.02)	0	0.06 (0.03)	11	14

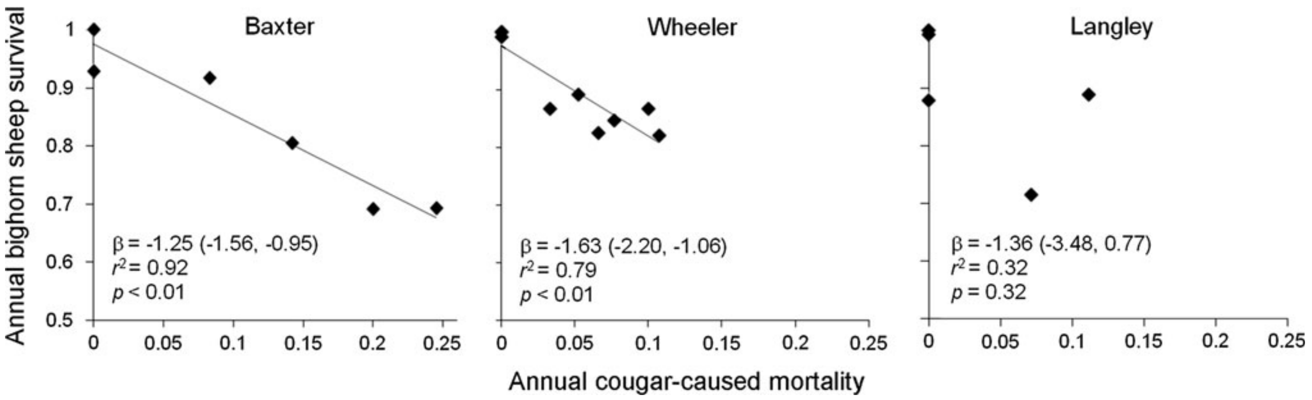

Fig. 3 Annual survival rates regressed against annual cougar predation rates in the Baxter, Wheeler, and Langley populations of Sierra Nevada bighorn sheep

Table 2 Winter habitat selection coefficients (±SE) from a multivariate model and from a univariate elevation model of each population of Sierra Nevada bighorn sheep, California, USA

Coefficient	Mono Basin	Wheeler	Langley	Baxter	Baxter: risk*date
Multivariate model					
Constant	−2.92 (0.10)	−3.69 (0.11)	−2.55 (0.09)	−3.79 (0.06)	−2.98 (0.07)
Slope	0.049 (0.003)	0.057(0.003)	0.039 (0.002)	0.062 (0.001)	0.062 (0.001)
Aspect	0.84 (0.05)	0.69 (0.03)	0.94 (0.03)	0.83 (0.02)	0.82 (0.02)
Ruggedness	40.50 (2.31)	8.26 (1.06)	6.92 (1.13)	14.50 (0.67)	14.56 (0.69)
Forest	−1.58 (0.11)	−0.70 (0.09)	−1.56 (0.07)	−1.12 (0.05)	−1.10 (0.05)
Risk	NA	0.0660 (0.0023)	1.1260 (0.0491)	0.1068 (0.0019)	0.0004 (0.0039)
Date	NA	NA	NA	NA	−0.0125 (0.0004)
Risk × date	NA	NA	NA	NA	0.0015 (<0.0001)
Univariate model					
Constant	−11.59 (0.44)	1.05 (0.10)	−0.55 (0.10)	1.38 (0.05)	NA
Elevation	0.0031 (0.0001)	−0.0008 (<0.0001)	−0.0002 (<0.0001)	−0.0009 (<0.0001)	NA

complex model), we found that selection for risk did indeed vary over the course of the winter and that the risk × date interaction improved model fit (Burnham and Anderson 2002; multivariate model: $\mathrm{AIC_C} = 40{,}646$, $k = 7$, pseudo $r^2 = 0.20$; multivariate + interaction $\mathrm{AIC_C} = 39119$, $k = 9$, pseudo $r^2 = 0.23$). As winter progressed, bighorn sheep increased their use of "high risk" habitat and decreased their use of "low risk" habitat (Fig. 5). Additionally, it appeared that bighorn sheep in populations with greater spatial overlap with deer (and at greater risk of encountering a cougar) selected "safer" terrain. Of the three populations with cougar predation, bighorn sheep selected for slope and terrain ruggedness in proportion to their overlap with deer (Fig. 4), such that bighorn sheep at Baxter used the steepest, most rugged terrain, followed by bighorn sheep at Wheeler and Langley, respectively. Bighorn sheep at Mono Basin, with no measurable risk of predation, did not select benign terrain but for intermediate slopes and highly rugged habitat (Table 2).

Of the habitat characteristics we examined, selection for elevation appeared to have the greatest power for predicting the degree of sympatry between bighorn sheep and deer. Univariate analyses showed that selection for low elevation habitat was directly associated with spatial overlap between bighorn sheep and deer and cougar predation. For example, Baxter selected the lowest elevation habitat and had the greatest overlap with deer and the highest cougar predation rates, followed by Wheeler and Langley, respectively. Mono Basin, the population that selected for high elevations, had no overlap with deer or cougar predation (Fig. 4; Table 2).

All habitat selection models had high predictive power when tested against out-of-sample GPS locations. Within 10 area-adjusted frequency bins of predicted habitat quality, Spearman rank correlations between expected and observed probabilities of selection were 0.89 for Mono Basin ($p < 0.001$), 0.98 for Wheeler ($p < 0.001$), 0.98 for Baxter ($p < 0.001$), and 0.70 for Langley ($p = 0.025$).

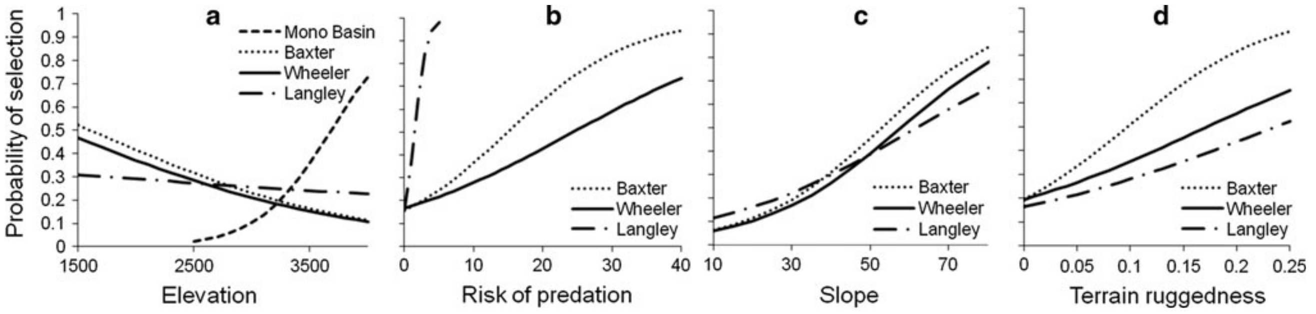

Fig. 4 Probability of selection for **a** elevation, **b** predation risk, **c** slope, and **d** terrain ruggedness for populations of Sierra Nevada bighorn sheep wintering in proximity to deer herds. Baxter has the greatest amount of spatial overlap with deer, followed by Wheeler, Langley, and Mono Basin, respectively. At Langley, risk of predation was only modeled for values <5 as this encompassed the range of possible risk values for this population. The lowest elevation available to bighorn sheep in Mono Basin is approximately 2,500 m

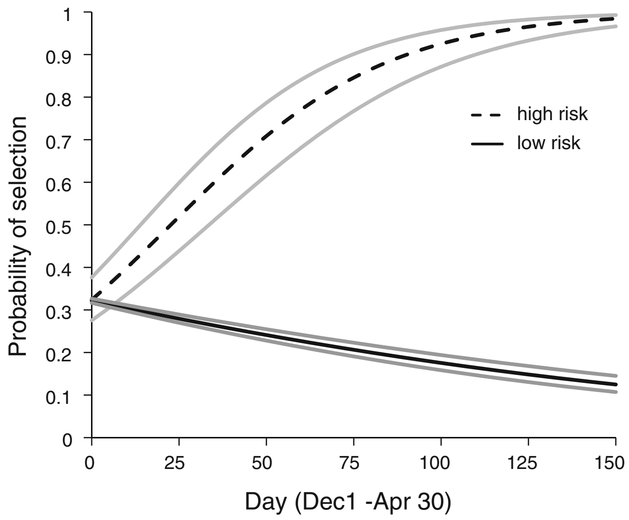

Fig. 5 Probability of selection for areas of low and high risk of cougar predation by Sierra Nevada bighorn sheep in the Baxter population over the course of the winter (December–April)

Discussion

Cougar predation on endangered Sierra Nevada bighorn sheep appears to be mediated by habitat overlap with mule deer in accordance with spatial predictions of apparent competition. Rates of cougar predation on bighorn sheep populations increased in direct proportion with the amount of overlap between bighorn sheep and deer winter ranges (Table 1), suggesting that sympatry between these species largely governs predation on bighorn sheep as secondary prey. The importance of spatial overlap between bighorn sheep and deer was further supported by the observation that 92 % of cougar-killed bighorn sheep were located within delineated deer winter range, even though that area only constituted a portion of the bighorn sheep winter range.

These patterns suggest that cougars kill bighorn sheep opportunistically when they inhabit the same hunting grounds as deer, their primarily prey source. While this kind of opportunistic take may be incidental to the prey-base of the predator, it can have a substantial influence on the dynamics of small prey populations (Courchamp et al. 2003; DeCesare et al. 2010). The recovery plan for Sierra Nevada bighorn sheep discusses cougar predation as a threat to bighorn sheep populations (US Fish and Wildlife Service 2007), but does not clearly acknowledge the role of deer or apparent competition in shaping this threat. By considering predation in the context of apparent competition, wildlife managers could better assess the vulnerability of bighorn sheep populations relative to the size and distribution of local deer herds.

Greater sympatry between bighorn sheep and deer was associated with higher predation rates on bighorn sheep, but also with increased additive effects of that predation on adult bighorn sheep survival (Fig. 3). For example, in Baxter, the population with the greatest spatial overlap with deer, annual cougar predation, and adult survival had a correlation coefficient of 0.92 indicating that variation in survival was primarily a function of variation in cougar-induced mortality. Between 2004 and 2010, mean annual survival for this herd was 0.84, but yearly rates varied dramatically between 0.69 and 1.0. In ungulates, annual adult survival should be high and fairly constant as this is the vital rate with the highest elasticity (Gaillard et al. 2000). Even a small change in adult survival will have a greater impact on population growth than the same proportional change in any other rate (Caswell 2001). Low annual survival and high variability in survival, as observed at Baxter due to predation, have been associated with declines in several other ungulate populations (Owen-Smith and Mason 2005; Wittmer et al. 2005; Johnson et al. 2010a; Bourbeau-Lemieux et al. 2011). Indeed, Baxter, Wheeler, and Langley have all experienced negative annual population growth rates in recent years, raising concern over additive sources of mortality in the recovery of this subspecies. If sources of additive mortality could be reduced in these small populations, there may be animals available for reintroductions allowing recovery goals to be sooner realized.

Although apparent competition appears to drive patterns of predation on Sierra Nevada bighorn sheep, it is important to recognize that the influence of predation was spatially variable among herds. Our estimates of cougar predation are conservative given that unknown mortality may have been due to cougars; however, average annual population-specific rates of cougar predation ranged between 0 and 0.12. While cougar predation may limit a population like Baxter, it certainly is not limiting a population like Mono Basin, or even Langley. Bighorn sheep in those populations do not have much spatial overlap with deer and cougars and primarily died of unknown causes. Indeed, Johnson et al. (2010b) found that survival and fecundity rates at Mono Basin were highly susceptible to Allee Effects and environmental stochasticity, suggesting that factors other than predation limit that herd. While cougar predation may not constrain population growth in all bighorn sheep herds, it does appear to constrain some herds; a key finding that is highly relevant to future management actions.

In addition to rates of cougar predation being spatially variable among herds of bighorn sheep, predation was also temporally variable across years. For example, annual rates of cougar predation on the Baxter population ranged widely from 0 to 0.24. Such variation has been observed in other populations of bighorn sheep, resulting in distinct temporal trends in population dynamics (Festa-Bianchet et al. 2006; Bourbeau-Lemieux et al. 2011). Patterns of such "stochastic" predation have been largely attributed to predators that begin specializing on secondary prey. Although some cougars may specialize on bighorn sheep in the Sierra Nevada, we suspect that small population sizes of bighorn sheep, and small sample sizes of collared animals in some years, exacerbated the observed variation in annual cougar predation. Despite this variation, trends in cause-specific mortality data suggest that the degree of spatial overlap between bighorn sheep and deer will serve as a useful predictor of population vulnerability to cougar predation.

We suspect that sympatry between bighorn sheep and deer was largely driven by differences in habitat selection among bighorn sheep herds. Indeed, as populations increased their selection for low elevation habitat, their spatial overlap with deer increased, and they suffered higher rates of cougar predation (Fig. 4). In a post hoc analysis, we calculated the amount of low elevation (<2,745 m), nonforested habitat available within the MCP areas of each population. Baxter had 32.8 km^2 of low elevation habitat available, Wheeler had 26.0 km^2, Langley had 5.4 km^2, and Mono Basin had just 0.1 km^2. These numbers suggest that bighorn sheep selected for low elevation habitat in accordance to its relative availability, showing a positive functional response for low elevation winter range (Mysterud and Ims 1998). Indeed, across these populations, we found a near-perfect relationship when we regressed the proportion of bighorn sheep winter range that overlapped with deer against the availability of low elevation habitat ($\beta = 0.021$, SE $= 0.001$, $r^2 = 0.99$, $df = 3$, $p = 0.003$). This suggests that, with greater availability of low elevation habitat, bighorn sheep increased selection for those areas, enlarged their spatial overlap with deer, and became more susceptible to the effects of predator-mediated apparent competition.

Habitat models also revealed that bighorn sheep selected for areas where they were at risk of cougar predation, rather than avoiding those areas. Wehausen (1996) concluded that Sierra Nevada bighorn sheep abandoned low elevation winter ranges due to cougar predation, remaining at high elevations where reduced access to forage may have depressed recruitment rates and contributed to population declines. In contrast, we found that bighorn sheep selected for areas of risk. This difference may be a function of the larger population sizes of bighorn sheep that are currently present, and corroborate several other recent studies that have found landscape-scale habitat selection among ungulates to be primarily based on topography and vegetation rather than on an avoidance of predators (Walker et al. 2007; Kittle et al. 2008; Valeix et al. 2009). In the Sierra Nevada, areas of high risk are also lower in elevation, higher in winter forage quality, and often overlap with deer. Positive coefficients for predation risk probably reflect selection for desired vegetation, not risk itself, reflecting a trade-off between forage quality and predation.

Although bighorn sheep selected for areas with a risk of predation, this selection was temporally variable over the course of the winter. A key result from our habitat analysis was that bighorn sheep in Baxter, the herd with the highest predation rate and overlap with deer, dramatically altered their use of risky habitat as the winter progressed (Fig. 5). In early winter, bighorn sheep showed little preference for risky habitat, perhaps because the energetic requirements for pregnant ungulates are minimal, body condition is adequate, and forage quality is generally low at all elevations (Parker et al. 2009; Greene 2010). By early spring (February–April in our study area), however, ungulates are at their poorest body condition and have high energetic costs associated with the last trimester of pregnancy. At the same time, green-up commences at lower elevations, and potentially draws bighorn sheep into areas of overlap with deer and cougars. Thus, nutritional demands likely exacerbate the impact of apparent competition, as sympatry between bighorn sheep and deer increases during late winter months, driving temporal variation in risk of predation within a season. We could only evaluate a risk-by-date model with data from Baxter, as the number of collared females afforded the degrees of freedom to fit a more complex model, but we suspect that similar patterns may exist in Wheeler and Langley.

While bighorn sheep did not avoid areas used by cougars, they did appear to mediate their risk through anti-predator behavior (Lima and Dill 1990). Populations that experienced predation selected “safer” terrain (i.e., more steep and rugged) in relation to their spatial overlap with deer (Fig. 4). Such selection patterns may allow bighorn sheep to forage in areas inhabited by cougars while partially mitigating their risk (Halofsky and Ripple 2008; Hebblewhite and Merrill 2009). Contrary to the other herds, bighorn sheep in Mono Basin did not exhibit expected patterns of habitat selection. Given that these bighorn sheep had no overlap with deer and no measurable cougar predation, we would expect them to select benign terrain relative to other herds. Instead, they showed the strongest selection for terrain ruggedness (Table 2). This pattern was likely a function of the limited availability of rugged terrain at the high elevations used by this population (Fig. 4), resulting in a high selection coefficient.

Evidence of apparent competition has important implications for the conservation and management of Sierra Nevada bighorn sheep. For populations of bighorn sheep that are highly sympatric with mule deer (i.e., Baxter), cougar predation may significantly limit population growth and recovery. Managers could potentially reduce predators and/or their primary prey source to alleviate this predation pressure (Lessard et al. 2005; DeCesare et al. 2010); however, these actions could yield untended consequences (i.e. the removal of cougars could result in higher deer densities, or the reduction in deer could exacerbate predation on bighorn sheep). Because cougar predation likely influences bighorn sheep during winter months in specific areas of deer overlap, cougar control could be targeted temporally or at the individual cougar level, minimizing the controversy regarding cougar removals among the broader California public. Additionally, managers could work to identify reintroduction sites where winter ranges of bighorn sheep are spatially de-coupled from deer and cougar populations. Indeed, our findings demonstrate that topographic and vegetation characteristics alone are inadequate for identifying high quality habitat for bighorn sheep in the Sierra Nevada, given the influence of deer and cougar populations. Reintroduction sites in areas of low deer density could serve as important refugia for bighorn sheep recovery, minimizing the need for continual management of predators or their primary prey (Sinclair et al. 1998). While predation via apparent competition may limit the recovery of some bighorn sheep populations (i.e. Baxter and Wheeler), it is not a limiting factor in all populations (i.e. Langley and Mono Basin). This observation emphasizes that the dynamics of small, endangered populations can be highly idiosyncratic, and that managers may need to identify population-specific recovery actions for conservation success.

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